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RESEARCH ARTICLE

An integrative taxonomic study of the genus *Lethocolea* (Marchantiophyta: Acrobolbaceae)

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Abstract

Background and aims – *Lethocolea* (Acrobolbaceae) is a small liverwort genus of seven species distributed in temperate regions of the Southern Hemisphere and on tropical mountains. The taxonomic history of the genus has been chaotic, the species were described under many different names and have been distinguished mainly based on geography. Here, we undertook a taxonomic revision of the genus based on a reassessment of morphological characters and a molecular analysis.
Material and methods – Type material and additional collections from 17 herbaria were examined in the morphological study. Sequences of the *rps4* chloroplast region and maximum likelihood analyses were used to reconstruct the phylogeny.
Key results and conclusions – Two fully supported clades were resolved within *Lethocolea* lending support to the recognition of two subgenera, subgen. *Lethocolea* and subgen. *Symphyomitra*. *Lethocolea congesta* from Africa, and *L. glossophylla* and *L. radicosa* from America exhibited considerable morphological overlap and were not distinguishable based on *rps4* sequences. The latter two species are reduced into synonymy with *L. congesta*, whose range spans across Africa, the Neotropics and southern South America. In Australasia, where only one species, *L. pansa*, is recognized, two morphotypes were found. The first one, with a smooth cuticle, wingless gemmae, and leaf cells without trigones, is identical to the type of *L. pansa* and occurs in Australia and New Zealand. In addition, the species is newly reported from South Africa. The second morphotype has a papillose cuticle, winged gemmae, and leaf cells with distinct trigones, and is assigned to *L. javanica*, which ranges across Australasia and furthermore occurs in Java and India. The recognition of these two species is supported by molecular analysis. Altogether, we recognize four species within *Lethocolea*, which are thoroughly described, illustrated, and keyed. We present 12 new lectotypifications.

Keywords

Afro-American distribution, Australasia, Lethocoleoideae, liverworts, molecular phylogeny, morphology, South Africa, taxonomy

INTRODUCTION

Lethocolea Mitt. (Acrobolbaceae subfam. Lethocoleoideae) is a small liverwort genus distributed in Mediterranean and temperate regions of the Southern Hemisphere and on tropical mountains, extending to the Holarctic in Japan and India. Because of its *Calypogeia*-type marsupium, presence of a calyptra, and the narrowly cylindrical capsule, the genus is classified in subfamily Lethocoleoideae together with *Goebelobryum* Grolle and

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Enigmella G.A.M.Scott & K.G.Beckm. (Schuster 2021) or in a monogeneric Lethocoleoideae (Briscoe and Engel 2016).

The taxonomic history of *Lethocolea* is chaotic and the species currently included in the genus have been described under many different names and in at least 11 genera, including *Calypogeia* Raddi, *Gongylanthus* Nees, *Gymnanthe* Taylor in Lehmann (1844), *Jamesoniella* (Spruce) F.Lees, *Jungermannia* L., *Lethocolea*, *Neoprasanthus* S.Winkl., *Odontoschisma* (Dumort.) Dumort., *Podanthe* Taylor, *Symphyomitra* Spruce, and *Tylimanthus* Mitt. The genus *Lethocolea* was established by Mitten (1867) based on *Gymnanthe drummondii* Mitt. (Mitten 1854) from New Zealand. The latter name is illegitimate as Mitten (1854) cited the older *Podanthe squamata* Taylor (Taylor 1846), described from Western Australia, as a synonym in the protologue of *G. drummondii*. The name *Lethocolea* has since been conserved (over *Podanthe*) (Zijlstra 1990; Turland et al. 2018).

Mitten (1867) distinguished *Lethocolea* by the procumbent plants with undivided leaves, without underleaves, and with a terminal marsupium. Following the reduction of *Symphyomitra* – described by Spruce (1885) to accommodate *S. glossophylla* Spruce from Ecuador – into the synonymy of *Lethocolea* (Grolle 1965), the genus was divided by Grolle (1965, 1972) into two subgenera, subgen. *Lethocolea* (marsupium long-cylindrical, gemmae present) and subgen. *Symphyomitra* (marsupium short-cylindrical, gemmae absent). The two subgenera were lowered to sectional level by Schuster (2021), as sect. *Lethocolea* and sect. *Pachycolea* R.M.Schust.

Currently, *Lethocolea* contains seven species: four in subgen. *Lethocolea* (*L. pansa* – Australasia (Fig. 1A); *L. javanica* Schiffn. – Java and S. India; *L. naruto-toganensis* Furuki – Japan; *L. indica* G.Asthana & Maurya – N. India) and three in subgen. *Symphyomitra* (*L. congesta* (Lehm.) S.W.Arnell – Africa (Fig. 1B); *L. glossophylla* (Spruce) Grolle – tropical America; *L. radicosa* (Lehm. & Lindenb.) Grolle – Chile and south Atlantic Islands) (Briscoe and Engel 2016; Gradstein 2024). Three further species have been assigned to *Lethocolea*: *L. amplexifolia* (Lehm.) Grolle (Neotropics), *L. prostrata* Mitt. (Tristan da Cunha), and *L. repens* S.Winkl. (Colombia); however, *L. amplexifolia* has been transferred to *Solenostoma* Mitt., as *S. amplexifolium* (Lehm.) Váňa & Schäf.-Verw., *L. prostrata* is a synonym of *L. radicosa* (Váňa and Engel 2013), and *L. repens* (type lost) is a possible synonym of *Gongylanthus liebmannianus* (Lindenb. & Gottsche) Steph. (Gradstein 2021).

Globally, knowledge of the taxonomy of *Lethocolea* remains very limited. Furuki (2001) tabulated the morphological differences among the recognized species, but the table indicated much overlap. Schuster (2021) considered the taxonomy of the genus "chaotic" and Grolle (1965) suggested the existence of perhaps only one, highly variable species. The species of *Lethocolea* have been distinguished mainly based on geography. Within subgen. *Symphyomitra*, *L. congesta*, *L. glossophylla*, and *L. radicosa* are restricted, respectively, to tropical and South Africa, to tropical America, and to southern South America, Tristan da Cunha, and Crozet Is. Morphological separation of these three species is fully unclear and species identification is based on geographical origin of the material. The tendency to recognize species based on geographic disjunctions prevailed during the period of active bryological exploration of extra-European regions in the 19th century, when hundreds of new "geographical species" were described based in large part on the assumption that populations from distant regions must represent different species (Gradstein et al. 1983; Shaw 2001). Perhaps as a reaction to over-splitting, the reverse trend prevailed during the 20th century, when disjunct taxa were lumped into broadly defined species with large, trans-oceanic distribution ranges (Shaw 2001). While molecular data provided some support for the latter hypothesis (Gradstein 2013; Flagmeier et al. 2021), instances of allopatric speciation within species, previously thought to exhibit large, disjunct ranges, has been increasingly reported. In fact, a review of bryophyte phylogeographic evidence suggested that, across studies, the number of speciation events largely exceeds that of transcontinental dispersal events to explain current patterns of disjunct species distributions (Patiño and Vanderpoorten 2018). All in all, the relevance of geography as a taxonomic character within *Lethocolea* thus remains to be tested.

Here, we undertook a taxonomic revision of *Lethocolea* based on a reassessment of relevant morphological characters in light of a molecular phylogeny of the genus, to test previous taxonomic hypotheses and to provide an up-to-date account on the species that should be recognized in the genus, their key characters and geographic range.

MATERIAL AND METHODS

Morphology

Type specimens and about 250 additional collections from 17 herbaria (BM, BOL, BR, CANB, CBG, FH, G, GOET, JE, MANCH, MO, NY, PC, PRE, QCA, U, and W) were examined. Leaf surface ornamentation was studied by light and scanning electron microscopy. Measurements in the morphological descriptions represent the complete variation of the plants.

Molecular analysis

Sequence data were obtained for five out of the seven species recognized in the genus, depending on the availability of sufficiently recent specimens for molecular analysis. For each species, 1–4 specimens were processed (Table 1). Representatives of five genera of Acrobolbaceae, i.e. *Acrobolbus ciliatus* (Mitt.) Schiffn., *Austrolophozia*

paradoxa R.M.Schust., *Conoscyphus trapezioides* (Sande Lac.) Schiffn., *Goebelobryum unguiculatum* (Hook.f. & Taylor) Grolle, and *Saccogynidium decurvum* (Mitt.) Grolle, were used as outgroups. After an initial screening of cpDNA loci on a subset of specimens, the locus *rps4* which exhibits a high species-specific variation in bryophytes (Liu et al. 2010; Ślipiko et al. 2020), was selected for exhibiting suitable variation among species in the genus. Sequences of *rps4* were either downloaded from GenBank or produced de novo (Table 1). DNA was extracted using a slightly modified CTAB protocol and amplified at the *rps4* locus using the primers rps5 and trnS (Wynns and Lange 2014). Sequences were edited with PhyDe v.0.9971 (Müller et al. 2006) and aligned with SeaView v.5.0.5 (Gouy et al. 2010). Seaview was employed to generate a Maximum Likelihood tree, implementing the GTR substitution model selected by ModelTest-NG v.0.1.7 (Darriba et al. 2020). Support for branches was assessed by implementing a non-parametric bootstrap analysis with 100 replicates.

Figure 1. Habit of *Lethocolea*. **A**. *L. pansa*. **B**. *L. congesta*. Photos: A by Bruce Fuhrer; B by Jan Peter Frahm.

RESULTS AND DISCUSSION

In the molecular analysis, *Lethocolea* was monophyletic without support. In view of the lack of a strong molecular support for the genus, the monophyly of *Lethocolea* should be re-assessed using a larger number of loci within Acrobolbaceae. Two fully-supported clades were resolved within *Lethocolea* (Fig. 2), lending support to the recognition of two subgenera as proposed by Grolle (1972). One clade, labelled in Fig. 2 as subgen. *Lethocolea*, included two accessions of specimens from Australia originally identified as *L. pansa* and labelled as *L. javanica*, and one accession of a specimen from South Africa originally identified as *L. congesta* and labelled as *L. pansa*. The second clade, labelled in Fig. 2 as subgen. *Symphyomitra*, included a large polytomy comprised of one accession of *L. congesta* from Réunion, four accessions of *L. glossophylla* from tropical America, and two accessions of *L. radicosa* from Chile.

Within subgen. *Symphyomitra*, *L. congesta*, *L. radicosa*, and *L. glossophylla* were not distinguishable based on *rps4* sequences. The study of herbarium specimens revealed considerable morphological overlap among the three species. All three species appeared to be dioicous; although Arnell (1963) described *L. congesta* as being paroicous (with a question mark), no paroicous specimens were observed and Arnell's observation must be considered erroneous. Specimens of all three species had ovate to ovate-oblong to lingulate leaves, being 1–2.2× longer than wide and with variation in leaf shape across their distribution range (Fig. 7). Leaf shape was particularly variable in Chile and plants with suborbicular leaves (1–1.2× longer than wide) or lingulate leaves (1.5–2× longer than wide) occurred within a single collection. Other leaf features proved to be variable as well and did not permit the separation of the species. Several authors suggested that *L. congesta* differs from *L. radicosa* and *L. glossophylla* in producing disciform gemmae (e.g. Arnell 1963; Grolle 1969; Gradstein et al. 1983; Schuster 2021). However, no evidence for occurrence of gemmae in *L. congesta* was found in this study (gemmiferous specimens of "*L. congesta*", all from South Africa, belong to *L. pansa*; see below), and the species appeared to be fully similar to *L. radicosa* and *L. glossophylla*. Altogether, our results indicate that *L. congesta*, *L. glossophylla*, and *L. radicosa* are conspecific. The morphological characteristics of the species – for which *L. congesta* is the correct (oldest) name – are tabulated in Table 2.

The subgen. *Lethocolea* clade included two Australian accessions originally identified as *L. pansa*, the only species reported from that continent, as well as one accession of a specimen originally identified as *L. congesta* and collected in South Africa. The latter plant clearly differed from *L. congesta* in having a fully smooth cuticle (papillose in *L. congesta*; Fig. 3A, B) and purplish stems (unpigmented in *L. congesta*). Moreover, the plant was gemmiferous. Study of collections made by Sigfrid Wilhelm Arnell in South Africa and kept in the Bolus Herbarium (Cape Town), revealed that the plants were identical to some of the paratypes of *Symphyomitra tabularis* S.W.Arnell, a species described from South Africa (Arnell 1953) and placed in the synonymy of *L. congesta* by Arnell (1955, 1963). Apparently, the type materials of *S. tabularis* were a mixture of *L. congesta* and the unknown gemmiferous plant with a smooth cuticle and purplish stem. Unexpectedly, study of the types of *L. pansa* and *L. squamata* from Australia showed that the gemmiferous South African plant is morphologically totally identical to the Australian plants. Although described as having a papillose cuticle (e.g. Scott 1985; Schuster 2021), the cuticles of the types of *L. pansa* and *L. squamata* (Western Australia, Swan River, *Drummond s.n.*) are totally smooth. Moreover, the plants have wingless gemmae and lack distinct trigones (Figs 4D–F, 5F–J).

We conclude that *Lethocolea pansa* is the correct name of the gemmiferous plant from South Africa; the geographic range of the species appears to span across Australasia to the Western Cape Province of South Africa. In spermatophytes, relationships between the Cape flora and Australia prevail (Galley and Linder 2006). Among bryophytes, the South African/Australian disjunction has been reported from various ephemeral moss genera such as *Archidium* Brid., *Bryobartramia* Sainsbury, and *Ephemerum* Hampe, the epiphytic genus *Stoneobryum* D.H.Noris & H.Rob., and the thalloid liverworts *Monocarpus* D.J.Carr and *Riccia* L. (Perold 1999; Hedderson 2012; Cargill 2022; Lara et al. 2023). A comparative analysis of the biogeographic similarities and relationships among the bryophyte floras of South Africa and Australia is recommended.

The South African accession of *Lethocolea pansa* is both molecularly and morphologically different from the two Australian accessions initially identified as *L. pansa*. They clearly differ from *L. pansa* in having a strongly papillose cuticle, leaf cells with distinct trigones, and winged gemmae with an irregularly crenate margin (Figs 3C, 4A–C, 5A–E). Study of type specimens indicated that the names *L. javanica* (Schiffner 1898; type from Java) and *Gongylanthus leratae* Steph. (Stephani 1922; type from New Caledonia) are available for the papillose Australian plants. It follows that *L. javanica* Schiffn. (= *Gongylanthus leratae* Steph., syn. nov.) is the correct name for the papillose Australian plants.

Our results thus reveal the existence in Australia of two species of *Lethocolea*, *L. javanica* and *L. pansa*, instead of one. Based on our study of herbarium specimens and literature, it appears that *L. pansa* is distributed in Australia and New Zealand and in addition occurs in South Africa, whereas *L. javanica* ranges across Australasia, from Australia to New Caledonia, and furthermore occurs in Java and southern India. The differences between these two species are summarized in Table 2.

No material for molecular analysis was available of the two other species of subgen. *Lethocolea*, viz. *L. naruto-toganensis* and *L. indica*. *Lethocolea naruto-toganensis*, known only from the type locality in Japan, appears to

Table 1. Voucher information and GenBank accession numbers of *Lethocolea* specimens used in this study; new sequences in bold.

Taxon	Voucher	Accession number
Acrobolbus ciliatus	*Long 30514* (E)	KF851435
Saccogynidium decurvum	*B. Shaw 6410* (DUKE)	KF851479
Austrolophozia paradoxa	*Engel & von Konrat 28538* (F)	KF851427
Conoscyphus trapezioides	*Renner 6986* (NSW)	MH108108
Goebelobryum unguiculatum	*Y. Qiu et al. 03054* (AK)	DQ787472
Lethocolea congesta	*Ah-Peng & Lavocat s.n.* (BR)	**PP886117**
L. glossophylla 1	*Söderström 2004/131* (BOL)	AM398245
L. glossophylla 2	*Davis 259* (DUKE)	AY608084
L. glossophylla 3	*Söderström 2004/047* (BOL)	AM398244
L. glossophylla 4	*Schäfer-Verwimp 32171* (JE)	**PP886118**
L. javanica 1	*Purdie 12476* (CANB)	**PP886113**
L. javanica 2	*Cargill 1772* (CANB)	**PP886114**
L. radicosa 1	*Larrain 43937* (BR)	**PP886115**
L. radicosa 2	*Larrain 45507* (BR)	**PP886116**
L. pansa	*Hedderson 15301* (BOL)	AM398267

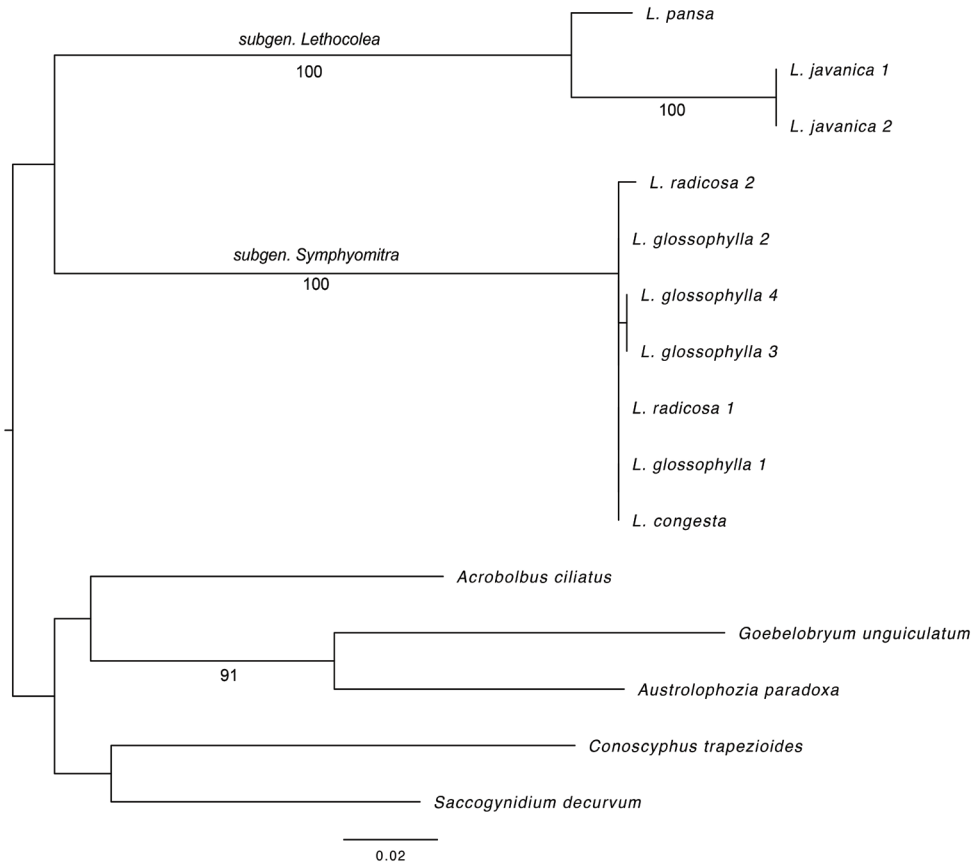

Figure 2. Maximum likelihood tree resulting from *rps4* sequences in the liverwort genus *Lethocolea*. Numbers below the branches correspond to bootstrap support.

be morphologically well-defined by its paroicous sex distribution (other *Lethocolea* species are dioicous), purple-red rhizoids, colourless oil bodies, and relatively short marsupia, up to 3 mm long. *Lethocolea indica* from northern India (Uttarakhand) was apparently described based on a mixture of *Lethocolea* and *Jackiella* Schiffn. (see taxonomic treatment) and is therefore considered a dubious taxon. Unfortunately, the holotype of the species was not available for study.

Table 2. Summary of diagnostic characters to distinguish the species of *Lethocolea*.

Character	*L. congesta*	*L. javanica*	*L. pansa*	*L. naruto-toganensis*
sexuality	dioicous	dioicous	dioicous	paroicous
rhizoid colour	hyaline to light brown	hyaline to light brown to pink	hyaline	purple-red
colour of stem underside	green	dark purplish-reddish	dark purplish-reddish	green
cuticle	papillose	papillose	smooth	smooth
trigones	distinct	distinct	indistinct	indistinct
colour of oil bodies	dark brown	greyish-brown	greyish-brown	colourless
number of oil bodies per cell	1–3	1	1	1
length of marsupium	up to 3 mm	up to 10(–20) mm	up to 10(–20) mm	up to 3 mm
gemmae	absent	present	present	present
margin of gemmae	–	winged, crenulate to crenate by angularly protruding cells	not winged, crenulate	not winged, crenulate
origin of gemmalings	–	from margin of gemmae	from centre of gemmae	from margin of gemmae

TAXONOMIC TREATMENT

Lethocolea Mitt. (Hooker 1867: 751, 753), nom. cons.

Podanthe Taylor (Taylor 1846: 413) – Type species: *Podanthe squamata* Taylor (= *Lethocolea pansa* (Taylor) G.A.M.Scott & K.G.Beckm.).

Type species. *Lethocolea drummondii* Mitt., nom. illeg. (= *L. pansa* (Taylor) G.A.M.Scott & K.G.Beckm.).

Description. Plants dioicous, rarely paroicous (*L. naruto-toganensis*), prostrate, pale green to yellowish-green to olive-green to brownish, sometimes reddish or purplish, little-branched, branching ventral-intercalary or (rarely) lateral-intercalary, ventral branches stoloniform. Stems rather fleshy, usually fragile and made up of thin-walled cells, sometimes rigid and with slightly thickened epidermal walls, epidermis cells similar in size to medullary cells, rarely slightly smaller, ventral region of stem sometimes with fungal hyphae inside the cells. Rhizoids scattered to slightly fascicled, hyaline to light brown to pink, rarely purplish (*L. naruto-toganensis*), sometimes with fungal hyphae. Leaves succubous, alternate, imbricate, lamina flat to convex, or concave with convex margins, undivided, suborbicular to ovate to ovate-oblong to lingulate, insertion line reaching dorsal midline of stem, apex rounded to truncate to emarginate, margins entire, sometimes with a border of thick-walled cells, dorsal leaf base not or shortly decurrent, ventral leaf base not decurrent, lower ventral half of the leaf lamina with an area of enlarged, hyaline cells with little or no chlorophyll. Leaf cells isodiametric to elongate, fully thin-walled or with very small to medium-sized trigones, trigones usually hyaline, rarely reddish, cuticle coarsely papillose or smooth; oil bodies large, 1–3 per cell, usually ellipsoid, dark brown to greyish-brown (exceptionally colourless), sometimes persistent in dried material. Underleaves absent. Androecia terminal or intercalary on main shoots, bracts saccate (not saccate in *L. naruto-toganensis*), antheridia 1(–6) per bract, antheridial stalk short, up to 7 cells long, irregularly biseriate. Gynoecia terminal on main shoots, female bracts in 2–4 pairs, bracts slightly larger than vegetative leaves (except for the inner ones), standing upwards or spreading outwards; perianth absent; archegonia ca 20–30 per gynoecium. Marsupia pendent, shortly to elongate cylindrical, up to 3–10(–20) mm long, green and with smooth surface when young, brown and with usually hairy surface when mature, marsupial canal narrow, lined by few or numerous large, elongate, papilliform, mucilaginous cells; archegonia, calyptra and developing sporophyte carried to the base of the marsupium, archegonia with a short neck. Setae whitish, up to 1.2 cm long after elongation, massive, made up of ca 70 rows of cells (Fig. 9D), with distinct trigones. Capsules cylindrical, scarcely wider than the seta, tip acute to apiculate (Fig. 9C), capsule dehiscence complete or incomplete, splitting to the base into 4 or in only 2–3 valves with two adjacent valves remaining partially connate, capsule wall 2–4-stratose (Fig. 9F), cell walls of the outer layer yellowish to reddish-brown, with small, orange to reddish-brown nodular thickenings evenly spaced along the outer longitudinal wall and turning into conspicuous thickening bands on radial walls, cell walls of the inner layers hyaline, without thickenings (seen in *L. congesta* only); elaters with 1–2 spirals (seen in *L. congesta* only), narrowly fusiform, 130–200 × ca 10 µm, surface finely punctate; spores isodiametrical, ca 25 µm in diameter, yellowish to brown, surface finely papillose. Asexual reproduction (subgen. *Lethocolea*) via large, disciform (sometimes angular-shaped) gemmae produced near the shoot apex on the dorsal stem surface or on the bases of the dorsal leaf margins, gemmae green to light brown, 1–5 mm in diameter, 4–20 cells across, biconvex, 5–6 cells thick in the middle and 1–2 cells thick at the margin, sometimes with a 1-celled stalk, with or without

transparent, unistratose wing; gemmalings sprouting from the centre or the margin of the gemmae.

Distribution. Widely distributed in Mediterranean and temperate regions of the Southern Hemisphere and in tropical mountains, extending northwards to Mexico, India, and Japan.

Habitat. On sandy, loamy, or peaty soils subject to desiccation, in shaded and exposed sites, along trails, on earth walls and on soil over rock, sometimes in swampy, wet habitats, or floating on water, becoming deeply reddish-maroon. The plants sometimes grow partly buried in the substrate and may become brownish, somewhat purplish or carmine when growing in exposed sites.

Notes. *Lethocolea* is readily recognized by: 1) creeping, little-branched leafy shoots with rather fragile stems made up of thin-walled cells, without or with one (or more) ventral stolons; 2) rhizoids scattered, hyaline to light brown to pink (exceptionally purplish); 3) leaves succubous, insertion line reaching dorsal midline of stem, alternate, imbricate, undivided, suborbicular to ovate-oblong to lingulate, with a broadly rounded apex, entire margins and an area of enlarged hyaline cells in the lower ventral half of the leaf; 4) leaf cells with or without trigones, trigones hyaline, cuticle coarsely papillose or smooth, oil bodies 1–3 per cell, large, finely granular, greyish-brown to dark brown; 5) underleaves absent; 6) gametoecia on main shoots; 7) sporophyte enclosed by a pendent marsupium at the shoot apex (perianth absent); 8) calyptra present, free, carried down the marsupial canal to the foot of the marsupium together with the unfertilized archegonia; 9) capsule cylindrical, tip acute to apiculate; 10) asexual reproduction by multicellular, disciform gemmae (in subgen. *Lethocolea*).

By its undivided succubous leaves, lack of underleaves, and rather large, finely granular oil bodies, one or two per cell, *Lethocolea* has been confused with *Jackiella* (Jackiellaceae), *Odontoschisma* (Cephaloziaceae), and *Solenostoma* (Solenostomataceae). The latter three genera are distinguished from *Lethocolea* by the absence of an area of enlarged-hyaline cells in the lower ventral half of the leaf and by the smooth or finely papillose cuticle covered by minute papillae much smaller than in *Lethocolea*. *Jackiella* and *Odontoschisma,* moreover, have dorsal leaf insertions usually not reaching the dorsal midline of stem, gametangia on short ventral branches, and asexual reproduction by small, 1–2-celled gemmae. The sporophyte is enclosed by a perianth in *Odontoschisma* and *Solenostoma*, and by a marsupium in *Jackiella*.

Based on the results of the morphological and molecular study, four *Lethocolea* species are recognized in two subgenera, subgen. *Lethocolea* and subgen. *Symphyomitra.* The two subgenera are distinguished by the presence or absence of disciform gemmae, the length and shape of the marsupium, and the incidence of papilliform cells lining the marsupial canal (Grolle 1972). The two groups are fully supported in the molecular analysis (Fig. 2). Schuster (2021) treated the two subgenera as sections, but in view of the strong molecular support for the two groups we do not accept Schuster's classification.

Sporophytes are rare in *Lethocolea*; the above description is based on two sporophytic collections of *L. congesta*, with additions from Spruce (1885) and Schuster (2021). The seta of *Lethocolea* is massive and the capsule is cylindrical with an apiculate tip (Fig. 9C, D), like in other members of Acrobolbaceae (Schuster 2021). The capsule of *L. congesta* is unusual, however, in opening to the base into 2–4 valves (with two adjacent valves sometimes remaining partially connate) and in having a thin, mostly 2-stratose wall, with limited 3–4-stratose areas (Fig. 9F) and no thickenings on the walls of the inner cell layers (Fig. 9G, I) (capsule opening to the base into 4 valves, wall 4–10-stratose and with thickenings in all cell layers in other Acrobolbaceae). Moreover, the elaters of *L. congesta* possess 1–2 spirals (Fig. 9B) (elaters bispiral in Acrobolbaceae). Data on capsule wall thickenings and elaters are still lacking for the other species of *Lethocolea*. The sporophyte of *Lethocolea* clearly needs more study.

Key to the subgenera of *Lethocolea*

1. Oil bodies 1 per cell. Cuticle smooth or papillose. Disciform gemmae produced. Marsupia long-cylindrical, up to 20 mm long, swollen at the tip when mature, marsupial canal lined by numerous large, papilliform cells. Australasia, Asia, South Africa..... ..... **I. *Lethocolea* subgen. *Lethocolea***
– Oil bodies 1–3 per cell (usually 2). Cuticle papillose. Disciform gemmae not produced. Marsupia conical-subcylindrical, up to 3 mm long, tapered towards the tip, marsupial canal lined by few papilliform cells. Africa, America..... ..... **II. *Lethocolea* subgen. *Symphyomitra***

Key to the species of *Lethocolea*

Note on the observation of papillae. Observing the papillae on the leaf surface may sometimes be difficult as they are colourless and not always well-developed throughout the leaf, and sometimes absent on leaf margins. Their presence should be checked by carefully scrutinizing the leaf surface from apex to base (either dorsal or ventral leaf surface, it does not matter), while turning the micro-screw slightly and slowly, and by using the diaphragm for optimization of the illumination.

1. Leaf surface papillose (plants usually rather dull in appearance). Leaf cells with distinct trigones, at least in the upper half of the leaf; 1–3 oil bodies per cell. Gemmae, when present (in *L. javanica*), with a fully transparent, 1(–2) cells wide unistratose wing at the margin..... **2**

– Leaf surface smooth (plants usually glistening in appearance). Leaf cells without or with very small trigones; only 1 oil body per cell. Gemmae, when present, without wing **3**

2. Ventral stem surface green to purplish-reddish. Oil bodies 1 per cell, greyish-brown. Gemmae present or absent. Marsupium up to 10(–20) mm long. Australasia, Java, southern India ..... **2. *L. javanica***

– Ventral surface of stem green, never purplish-reddish. Oil bodies (1–)2–3 per cell, dark brown. Gemmae never produced. Marsupium up to 3 mm long. Africa, Central and South America, south Atlantic Islands ..... **4. *L. congesta***

3. Rhizoids purple-red. Oil bodies colourless. Marsupium up to 3 mm long. Paroicous. Japan (Honshu) ..... **3. *L. naruto-toganensis***

– Rhizoids hyaline. Oil bodies greyish-brown. Marsupium up to 10(–20) mm long. Dioicous. Australasia, South Africa ..... **1. *L. pansa***

I. ***Lethocolea*** subgen. ***Lethocolea***

Lethocolea sect. *Lethocolea*

Description. Stems ventral surface green or dark purplish-reddish pigmented; stolons present or absent. Leaf cells with smooth or densely papillose cuticle; oil bodies one per cell (Fig. 3E, F), ellipsoid, ca 10–25 µm long, greyish-brown, rarely colourless (*L. naruto-toganensis*), finely papillose, sometimes with 1–3 pupils or "eye spots" (= larger and lighter-coloured granules). Antheridia one per bract. Marsupia usually long and slender, narrowly cylindrical, (3–)8–15 mm long, when mature with swollen tip (Fig. 6B), wall 5–6 cells thick, marsupial canal lined by numerous elongate, papilliform cells that nearly fill the canal. Capsules splitting to the base into 4 valves. Asexual reproduction by disciform gemmae produced near the shoot apex on the dorsal surface of the stem or on the base of dorsal leaf margins (*L. naruto-toganensis*), gemmae 4–20 cells across, 0.1–0.5 mm in diameter, biconvex, becoming thinner to the margin and sometimes with a 1–2 cell wide unistratose, transparent wing.

Distribution. Three species in Australasia, Java, India, Japan, and South Africa.

1. *Lethocolea pansa* (Taylor) G.A.M.Scott & K.G.Beckm. (Scott and Beckmann 1987: 212)

Figs 1, 3–6

Jungermannia pansa Taylor (Taylor 1846: 275) – Type: same as for *Lethocolea pansa*.

Podanthe squamata Taylor (Taylor 1846: 413) – Type: AUSTRALIA – **West Australia** • Swan River; 1843; *Drummond s.n.*; lectotype (designated by G. A. M. Scott, in Zijlstra 1990): BM [BM000969499]; isolectotypes: BM [BM000969500], BM [BM000969524], FH [FH01122547].

Calypogeia squamata (Taylor) Spruce (Spruce 1882: 94) – Type: same as for *Podanthe squamata*.

Lethocolea squamata (Taylor) E.A.Hodgs. (Hodgson 1958: 582) – Type: same as for *Podanthe squamata*.

Gymnanthe drummondii Mitt. (Mitten 1854: 144), nom. illeg. – Type: NEW ZEALAND – **North Island** • "forests of Titiokura" (fide Mitten 1854); c. marsup.; *Colenso 3649*; lectotype (**designated here**): NY [NY04461792]. The other syntype (*Colenso 3681*, NY) is *L. javanica*.

Lethocolea drummondii Mitt. (Mitten 1877: 190), nom. illeg. – Type: same as for *Gymnanthe drummondii*.

Podanthe drummondii Gottsche (Gottsche 1880: 54) – Type: same as for *Gymnanthe drummondii*.

Symphyomitra drummondii (Gottsche) Steph. (Stephani 1901: 1123) – Type: same as for *Gymnanthe drummondii*.

Type. AUSTRALIA – **West Australia** • Swan River; on clay; s.d.; *Drummond s.n.*; lectotype (**designated here**): FH [FH01122546]; isolectotype: BM [BM013763002].

Description. Plants dioicous, 1–2 cm long, 1–3 mm wide, creeping, flaccid, glossy green to purplish when fresh, usually brownish in herbarium, with or without a short ventral stolon near the base, lateral branches scarce, innovations not observed. Stems ca 0.2–0.4 mm in diameter, rather fleshy and fragile, made up of large, thin-walled cells, upper surface green to brownish-green, ventral surface usually dark purplish-reddish. Rhizoids scattered, hyaline. Leaves present throughout the stem, succubous, imbricate, obliquely to widely spreading, somewhat asymmetrically ovate to ovate-oblong, 0.9–1.6 × 0.6–1.2 mm, ca 1.5× longer than wide, flat or slightly concave, usually unpigmented, occasionally with some brownish-purple pigmentation in older portions of the stem, apex broadly rounded, dorsal and ventral bases not decurrent. Leaf cells thin-walled, without or with very small trigones, less than 3 µm in diameter, sides of trigones concave (not bulging outwards), subrectangular, in the ventral and basal part of the leaf much larger than in the dorsal and apical part, dorsal cells 30–50 × 20–35 µm, ventral cells 40–100 × 30–50 µm, towards the leaf base over 100 µm long; margin cells slightly smaller, subquadrate, ca 25–30 µm; cuticle smooth; oil bodies (degenerated in herbarium material) always one per cell, ca 10–20 µm long, greyish-brown. Androecia terminal, bracts in 3–4 pairs, base saccate; antheridia one per bract, ovoid, with a short, biseriate stalk. Gynoecia bracts in 3–5 pairs, slightly larger than vegetative leaves (except for the smaller inner bracts at the mouth of the marsupium), spreading outwards, flat, dorsal margin somewhat undulate. Marsupia linear, green to greenish-brown, with almost smooth surface, up to 10 mm long, ca 0.5 mm in diameter, marsupial canal lined by numerous large, elongate, papilliform cells. Sporophytes not observed. Gemmae positioned on the dorsal stem surface or in leaf axils near the stem apex, dull green to light brown, orbicular to slightly longer than wide, 0.2–0.4 mm in largest diameter, 8–20 cells across, biconvex, 5–7 cells thick in the middle, 1–2 cells thick at the margin, cells subisodiametric, ca 25 µm in diameter, margin cells not

or partially transparent only, not forming a distinct wing, outer wall convex but usually not protruding outwards (exceptionally one or two cells protruding outwards), margin of gemmae crenulate. Gemmalings common, much more slender than ordinary plants, originating from the centre of the gemmae and consisting a long, almost colourless, almost bare microphyllous shoot terminating in a few densely imbricate leaf pairs.

Distribution. Australia, New Zealand, South Africa. The distribution of *Lethocolea pansa* in Australia and New Zealand needs further study as part of the published records from these countries (e.g. Engel and Glenny 2019; Schuster 2021), viz. plants with a papillose cuticle, distinct trigones, and winged gemmae, belong to *L. javanica* (see below). As shown here, published records of *L. pansa* from New Caledonia (Stephani 1922 as *Gongylanthus leratae*; Hürlimann 1974, 1985) belong to *L. javanica* as well.

Habitat. On bare, moist soil along trails, on road cuts and in open, mesic woodlands and scrub, also on soil over sandstone rock and near water, ca 150–1000 m. Scott (1985) noted that *Lethocolea pansa* may have the widest ecological tolerance of any Australian liverwort, "growing in dry and hot at one extreme, but found as a floating aquatic at the other extreme, and all stages between", but Scott and Beckmann (1987) found that records from very dry habitats belonged to *Gongylanthus scariosus* (Lehm.) Steph. Moreover, the present study shows that part of the published records of *L. pansa* from Australasia refer to *L. javanica*.

Additional material examined. AUSTRALIA – **New South Wales** • Kyeamba Travelling Stock Reserve South of Tarcutta; 356 m; c. gemm.; *Purdie 8216A*; CANB [CANB800536] • Weddin State Forst, 17 km SW of Grenfell; *Curnow 1850*; CANB [CANB8900876] • Lachlan Range State Forest, 15 km NW of Rankins Springs; c. gemm.; *Curnow 3367*; CANB [CANB9404944] • Goonoo State Forest, 5 km E of Mogriguy Forest Road, ca 23 km direct NNE of Dubbo; c. gemm.; *Curnow 6567*; CANB [CANB672034] • Goonoo State Forest, 3 Corners road, 1.5 km W of Dubbo – Mendooran road; c. gemm.; *Curnow 6597A*; CANB [CANB672077]. – **Northern Territory** • NE Arnhem Land, Gore, Rindarry Creek; *Russell-Smith 4829*; CBG [CBG8803914]. – **Queensland** • Silver Valley Road, 4.4 km by road SW of Herberton; c. gemm.; *Curnow 6871*; CANB [CANB898903]. – **South Australia** • Kangaroo Is., Western River Conservation Park, Waterfall Creek, 30 km ENE of Cape Borda; *Streimann 54953*; CBG [CBG9511339]. – **Western Australia** • Serpentine National Park, 2.5 km S of Jarrahdale; 150–200 m; *Pócs 04143/M*; EGR • Darling district, Perup Ecological Reserve; *Cargill 665*; CANB [CANB7590021] • Bullfinch Evanston Road, 69.3 km (by road) N of Bullfinch; *Curnow WA118*; CANB [CANB879890] • Karolin Rock, 20 km (by road) NW of Bullfinch; *Curnow WA130*; CANB [879902] • North Boundary Road, ca 3 km N of Kingston Road, ca 5 km E of Yornup; *Cargill 1200WA*; CANB [CANB900850] • 'Grevillea Rock', ca 25 km by road SE of Bridgetown, ca 1 km N towards Winnejup; *Cargill 685GR*; CANB [CANB759031].

SOUTH AFRICA – **Western Cape Province** • Kasteel Poort; *Arnell 1031*; BOL • Kasteel Poort; *Arnell 1036;* paratype of *Symphyomitra tabularis*; G • Constantia slopes; *Arnell 323*; BOL, JE (2 colls.) • Constantia slopes; *Arnell 387*; BOL • Constantia Nek; *Arnell 316*; BOL • Track from Constantia Nek to Table Mountain; 630 m; *Arts 129/11*; BR [BR5040313689887] • De Hoek, North foot of Zitzikanna Mts near Joubertina; ca 550 m; c. gyn.; *Esterhuysen 27343*; BOL • Riviersonderend Mts, Boesman's Kloof, path below De Galg; ca 1000 m; *Hedderson 15268b*; BOL • Swellendam-Ashton area, W slopes of Langeberg, Sitruspoort farm; ca 600 m; c. gyn.; *Hedderson 15301*; BOL.

Notes. *Lethocolea pansa* is characterized by the glossy green to brown (occasionally purplish) plants with dark purplish-reddish ventral stem surfaces, hyaline rhizoids, very thin-walled leaf cells without or with very small trigones, smooth cuticles, a single greyish-brown oil body per cell, up to 10 mm long marsupia, and dull green to brownish gemmae, 8–20 cells across, with a crenulate margin and no wing. *Lethocolea pansa* has been confused with *L. javanica*, which had been included as a synonym in *L. pansa* by recent authors following Grolle (1965, as *L. squamata*). *Lethocolea javanica* differs from *L. pansa* in the dull green (shaded sites) to carmine-red (exposed sites) plant colour, leaf cells with distinct trigones and a densely papillose cuticle (to be studied carefully: in older herbarium material the papillae may be somewhat inconspicuous), and smaller, pale-green gemmae with a strongly crenate margin and 1–2 cell wide transparent wing (Figs 3–5). Scott and Beckmann (1987), moreover, found that gemmalings of *L. pansa* germinated from the centre of the gemmae, supporting the earlier findings of Goebel (1906) from plants he had identified as *L. drummondii*. In contrast, gemmae of *L. javanica* (identified as *L. squamata*) germinated from the margins. Due to the densely papillose cuticle and the well-developed trigones, *L. javanica* is a more dull-coloured plant than *L. pansa*, and more rigid. The detailed description and illustration of *L. pansa* in Engel and Glenny (2019) is a combination of *L. javanica* and *L. pansa*.

The leaves in *Lethocolea pansa* are ovate to ovate-oblong (1.0–1.7: 1), but in one collection from Serpentine National Park, Western Australia (*Pócs 04143/M*), they are ovate-orbicular to narrowly lingulate, becoming increasingly elongate towards the base of the shoots. As a result, the outline of these plants is more or less triangular.

Lethocolea pansa resembles *L. naruto-toganensis* from Japan in the smooth cuticle and the wingless gemmae; the latter species differs from *L. pansa* in having purplish rhizoids, green stem undersides, colourless oil bodies, and paroicous sex distribution. Moreover, the gemmalings of *L. naruto-toganensis* originate from the margins of the gemmae (Furuki 2001), while those of *L. pansa* originate from the centre.

Lethocolea pansa is newly recorded here from South Africa, where it was previously labelled as *L. congesta* or *Symphyomitra tabularis* (Arnell 1953). The latter species was described based on a mixture of *L. congesta* and *L. pansa*, and was placed in the synonymy of *L. congesta* by Arnell (1955, 1963). *Lethocolea congesta* clearly differs from *L. pansa* in the rather dull-coloured, green to yellowish-green to yellowish-brown plants with unpigmented stems (but leaves may occasionally be tinged purple), leaf cells with trigones, a densely papillose cuticle, and 1–3 dark brown oil bodies per cell (usually 2) (Figs 1, 3) The marsupia of *L. congesta* are significantly shorter than those of *L. pansa*, up to maximally 3 mm, and the marsupial canal is lined by few large, papilliform cells. Gemmae are absent in *L. congesta*; all reports of gemmae in *L. congesta* (e.g. Arnell 1963; Grolle 1969; Gradstein et al. 1983; Schuster 2021) are erroneous and refer to *L. pansa*.

2. *Lethocolea javanica* (Schiffn.) Grolle (Grolle 1965: 83)
Figs 3–5

Symphyomitra javanica Schiffn. (Schiffner 1898: 193) – Type: same as for *Lethocolea javanica*.

Gongylanthus leratae Steph. (Stephani 1922: 257), **syn. nov.** – Type: NEW CALEDONIA – **Ile des Pins** • "De la 3e à la 4e commune par la Baie puante"; May 1909; c. marsup. & andr.; *L. Lerat 67*; lectotype (**designated here**): G [G00067194]; isolectotype: JE • "Route de Wahehia à la Mission"; Jun. 1909; *L. Lerat 74*; syntype: G [G00051144].

Type. INDONESIA – **West Java** • "Pov. Preanger. In Cinchoneto "Daradjat" prope Garut ad terram. Regio nubium"; ± 1730 m; 2 Feb. 1894; c. marsup.; *V. Schiffner 499*; lectotype (**designated here**): FH [FH01122545]; isolectotypes: G [G00064407], JE.

Description. Plants dioicous, 1–2 cm long, 0.5–2 mm wide, prostrate, somewhat dull-coloured (due to the densely papillose cuticle), pale green to olive green to light brown (shaded sites) or carmine red (exposed sites), shoots in strongly exposed sites worm-like with densely imbricate leaves, in shaded sites more flattened and with spreading, less densely imbricate leaves, stolons usually absent, when present located near the base of the shoot, leafy branches and innovations not observed. Stems ca 0.2–0.4 mm in diameter, fragile or rigid; dorsal surface green, ventral surface green or purplish-reddish; epidermal and medullary cells similar in size of the epidermal cells slightly smaller (Schuster 2021, as *L. pansa*), all cell walls thin (stems fragile) or walls of the epidermal cell walls slightly thickened (stems rigid). Rhizoids scattered, hyaline to light brown (to reddish or pink; Schuster 2021), with thin walls, sometimes with fungal hyphae. Leaves succubous, imbricate, unpigmented to partially or almost entirely brown to reddish pigmented, obliquely to widely spreading, subvertically arranged and appressed to spreading outwards or obliquely to widely spreading outwards, flat to convex to concave with convex margins, ovate-orbicular to broadly ovate to ovate-oblong (1.0–1.7:1), apex broadly rounded, margins entire, dorsal and ventral bases not or slightly decurrent. Leaf cells in the upper and dorsal part of leaf rounded-isodiametrical to slightly elongate, ca 20–30 μm in diameter, towards the margin similar in size or smaller, subquadrate, border of thicker-walled cells lacking, cells in the lower central and ventral part of the leaf distinctly enlarged, becoming 2–3× larger and more hyaline than in the upper part of leaf, isodiametrical to elongate, 1–4(–7)× longer than wide, becoming increasingly elongate towards the lower ventral margin; cells with distinct trigones, the trigones 3–8 μm in diameter, fully hyaline, sometimes reddish, with concave to slightly bulging sides, sometimes seemingly vanishing towards the ventral base, in the enlarged cells; cuticle of dorsal and ventral surface of leaf covered by low, hyaline, rounded to elongate papillae, the papillae becoming progressively more elongate towards the leaf base and sometimes rather inconspicuous in older herbarium material, when rounded ca 3–6 μm in diameter, cuticle at leaf margin smooth or with low papillae; oil bodies one per cell, greyish-brown, sometimes persistent in old herbarium material, finely papillose and sometimes with 1–2 pupils ("eye spots"), spherical to ellipsoid, 8–20(–25) μm long, ca 1/3–1/2 the length of the cell-lumen in the upper half of the leaf, in the lower half of the leaf cells only ca 1/5–1/4 the length of the lumen in the enlarged leaf cells. Underleaves not observed (Schuster 2021: occasionally present on some stems, ovate-elliptical to ligulate). Androecia with 5–6 pairs of bracts, bracts saccate, antheridia one per bract. Gynoecia as in *L. pansa*. Marsupia up to 10(–20) mm long, sometimes shorter (only ca 2.5 mm long in *Pócs 01113/A* from northern Queensland), outer surface hairy, wall 5–6 cells thick, marsupial canal lined by numerous large, somewhat clavate, papilliform cells, the cells up to 75 μm long, 13–20 μm wide, protruding from the mouth of the marsupium. Sporophytes (Schuster 2021) foot massive, with an extensive haustorial collar; seta long and slender; capsule narrowly cylindrical, hardly wider than the seta, slightly pointed or beaked at apex, opening by four valves. Gemmae positioned on the dorsal stem surface near the shoot apex, pale green, orbicular to slightly elongate, 4–10(–15) cells across, pale green to yellowish-brown, biconvex, centre up to 6 cells thick, towards the margin transparent, forming a 1(–2) cell wide unistratose wing, outer margin crenulate to irregularly crenate due to angularly protruding cells. Gemmalings originating from the margin of the gemmae.

Distribution. Australasia (Australia, New Zealand, New Caledonia), Indonesia (Java), southern India (Kerala: Nilgiri Hills, Tamil Nadu). In Indonesia, *L. javanica* is known from two old collections from Java; its occurrence on soil along trails suggest that the species should be more common in Indonesia and has been overlooked. The true distribution of *L. javanica* and *L. pansa* in Australia and New Zealand requires more study and is beyond the limits

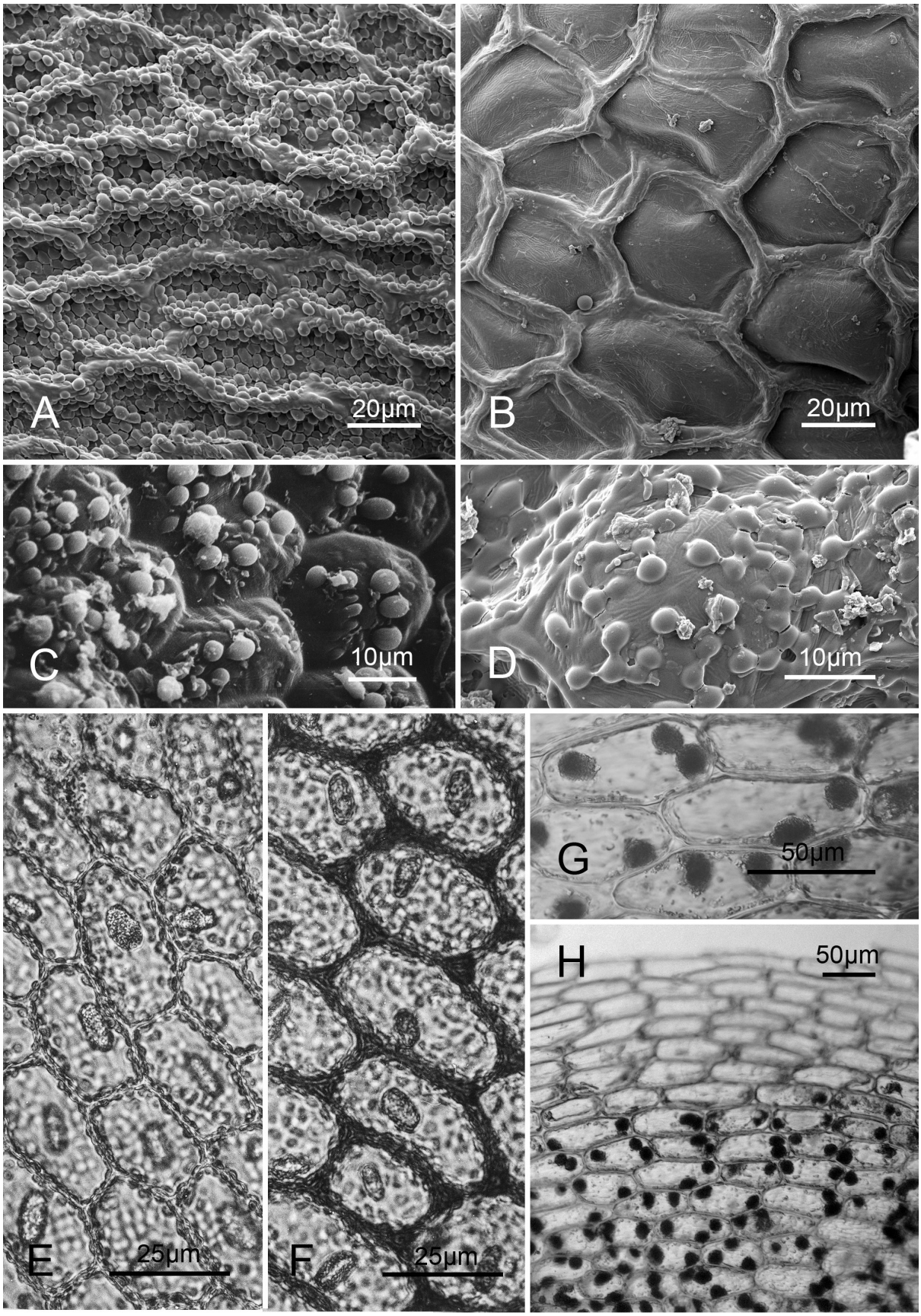

Figure 3. Cuticle and oil bodies in *Lethocolea*, SEM. **A**, **D**. Papillose cuticle of *L. congesta*. **B**. Smooth cuticle of *L. pansa*. **C**. Papillose cuticle of *L. javanica*. **E**–**F**. Oil bodies of *L. javanica*. **G**–**H**. Oil bodies of *L. congesta*. A, D from *Larrain 42566*; B from *Arts 129/11*; C, E–F from Beckmann (unpublished thesis work, 1985); G–H from from *Arts 19/54*. Photos: A–B, D by Anna Luiza Ilkiu-Borges; C, E–F by Karen Beckmann; G–H by Christine Cocquyt and Robbert Gradstein.

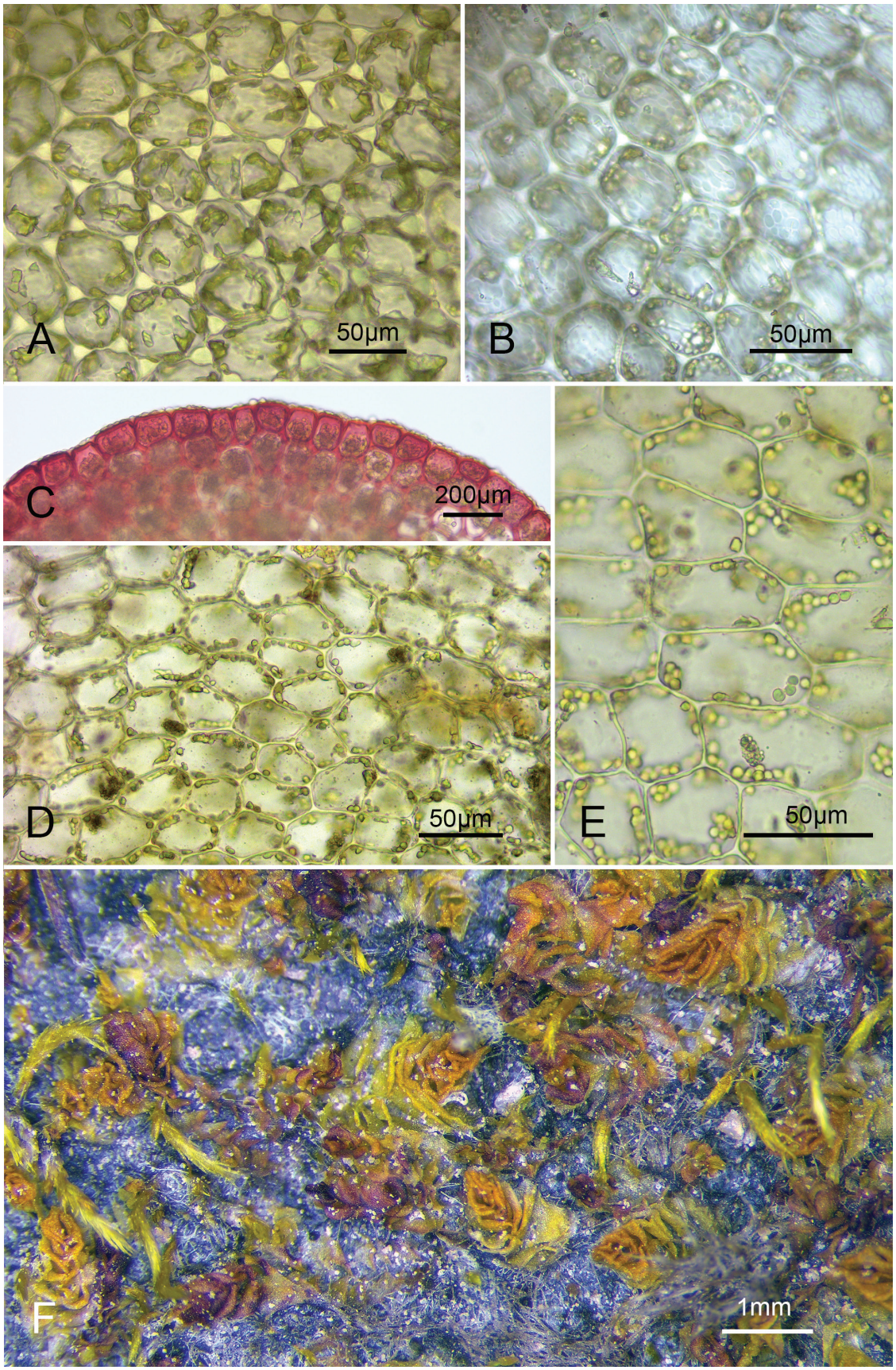

Figure 4. Leaf cells and habit of *Lethocolea javanica* and *L. pansa*. **A**–**B**. Midleaf cells of *L. javanica,* showing large trigones. **C.** Leaf margin cells of *L. javanica,* showing papillae. **D**–**E**. Midleaf cells of *L. pansa,* showing trigones absent or very small. **F**. Habit of *L. pansa* (wetted herbarium material). A–B from *Cargill 166*; C from *Docherty 2*; D from *Purdie 8216A*; E from *Curnow 6597A*; F from *Purdie 8216A*. Photos by D. Christine Cargill.

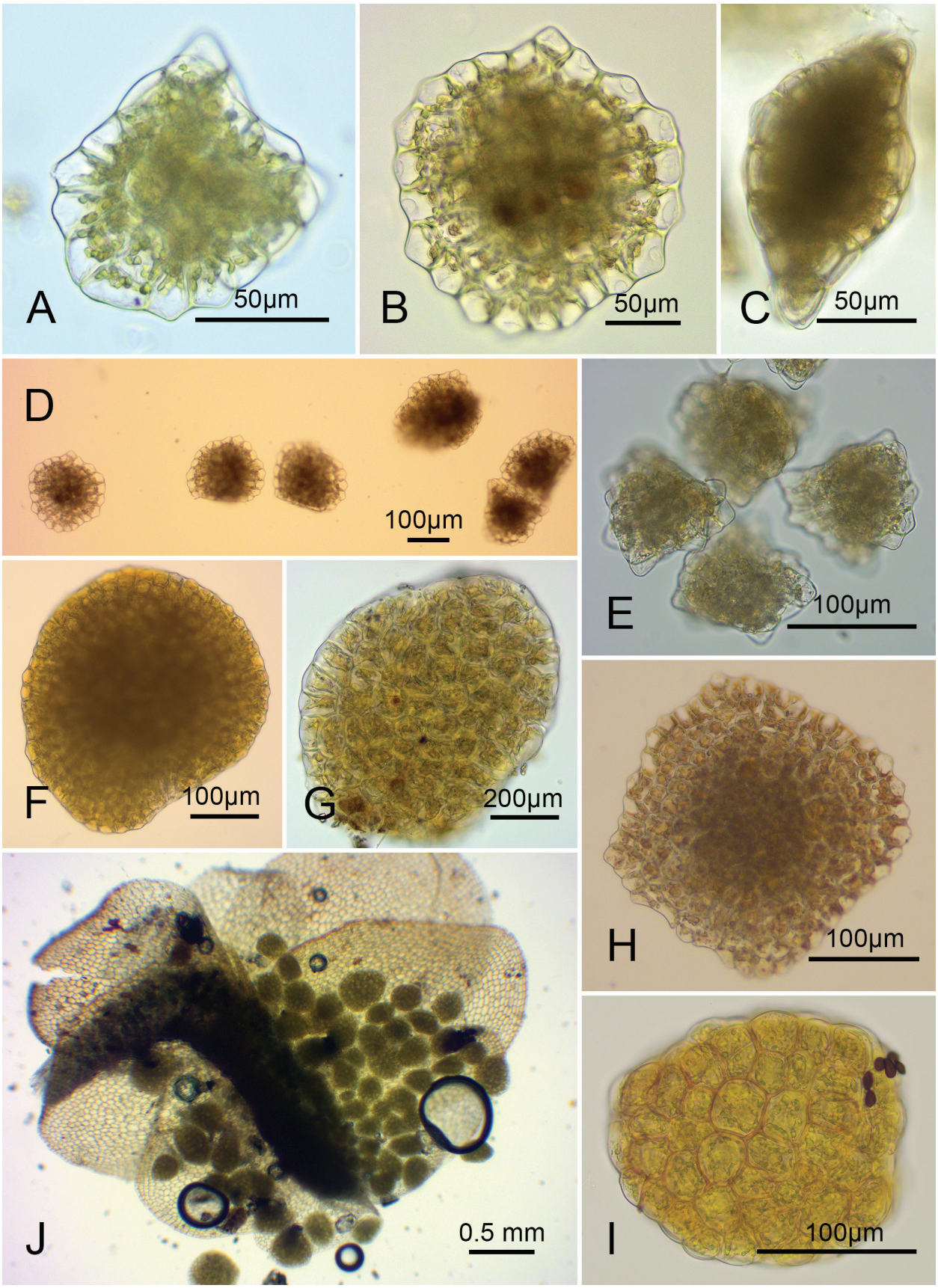

Figure 5. Gemmae of *Lethocolea javanica* and *L. pansa*. **A**–**E**. Winged gemmae of *L. javanica*. **F**–**J**. Wingless gemmae of *L. pansa*. A from *Streimann 970*; B–D from *Streimann 49251*; E from *Curnow 6163*; F from *Curnow 6871*; G from *Purdie 8216A*; H from *Curnow WA118*; I from *Curnow 6567*; J from *Streimann 54953*. Photos by D. Christine Cargill.

of the present study. For the occurrence of *L. javanica* in India see Udar and Kumar (1986) and Alam (2014).

Habitat. *Lethocolea javanica* grows on shaded and exposed sandy, loamy, or peaty soil, or soil over rock which dries out periodically, in rather xeric to humid vegetation, often along trails or water courses, from almost sea level to ca 1000 m in Australasia, and at 1700–2000 m in tropical Asia. In New Caledonia, the species occurs on basic, serpentine soil (pH 5–6) in maquis-type vegetation.

Additional material examined. AUSTRALIA – **Australian Capital Territory (A.C.T.)** • Canberra, Canberra National Herbarium, greenhouse collections; *Cargill 1772*; CANB • Canberra, Canberra National Herbarium, greenhouse collections; *Purdie 12476*; CANB. – **New South Wales** • Jimberoo State Forest, 11 km NNE of Rankin Springs; *Curnow 3376*; CANB [CANB9404956] • Cottan-Bimbang National Park, 0.5 km from Cells and 3 km from Oxley Highway; c. gemm.; *Curnow 6163*; CANB [CANB889563] • 19 km from Batemans Bay on Braidwood Road; 300 m; *Streimann 970*; CBG [CBG054175] • Weddin Mountain National Park, 16 km SW of Grenfell; *Streimann 49251*; CBG [CBG9213766]. – **Northern Territory** • NE Arnhem Land, Gore, Rindarry Creek; 40 m; *Russell-Smith 4829*; JE. – **Queensland** • Paluma Range, forest road 1–2 km N of Mt. Zero; 950 m; c. marsup.; *Pócs 01113/A*; GOET • Paluma Range, along Taravale forest road E of Mt. Zero; *Cargill 165*; CANB [CANB644649]. – **Western Australia** • Darling Range, forest at Martin, Mills Road, 22 km SE of Perth; *Curnow 4793*; CBG [CBG9512491] • D'Entrecasteaux National Park, 315 km S of Perth; *Cargill 722*; CANB [CANB759070].

NEW ZEALAND – **North Island** • "Forests of Titiokura" (Mitten 1854); c. marsup.; *Colenso 3681*, syntype of *Gymnanthe drummondii* Mitt.; NY [NY04461793] • Taupo; c. marsup.; *Berggren 3141*; NY [NY04461794] • Near Atiamuri; 1200 ft.; oil bodies persistent; *Allison H259*; JE • Hawkes Bay, Wairoa, Kiwi Valley; c. marsup.; *Hodgson 6454*; JE • Unuwahu bush; 300 m; *Bartlett 2-79-4*; JE • Ahipara; 200 m; *Bartlett 195*; JE •

NEW CALEDONIA – **Grand Terre** • Mont-Dore, near bifurcation of road Yaté–Plum; ca 100 m; c. andr.; *Hürlimann 2001*; GOET, PC • same data as for preceding; *Hürlimann 2002*; GOET, PC • East of Yanna valley near St. Louis; ca 150 m; *Hürlimann 2013*; GOET • same data as for preceding; *Hürlimann 2033*; GOET • Valley of Pouéta Kouré above La Coulée; 55 m; *Hürlimann 2035*; GOET, PC • Crest of Koghis Mts, SE of Mt. Bouo; 710 m; *Hürlimann 2127*; GOET, PC • Mt. des Sources; ca 800 m; *Hürlimann 2354*; GOET, PC • Dumbéa, near "Sunshine" mine; ca 650 m; c. gemm., oil bodies persistent; *Hürlimann 2409*; GOET.

INDONESIA – **Java** • Central Java, Salangan; 1924; c. gemm.; *Goebel s.n.*; JE.

Notes. *Lethocolea javanica* is recognized by the densely papillose cuticle, distinct trigones in the middle and upper part of the leaves, and winged gemmae with a crenulate to crenate margin of slightly to strongly and angularly protruding cells. In Australasia, the species has previously been called *L. pansa* (e.g. Engel and Glenny 2019; Schuster 2021), but the latter species has a smooth cuticle, minute trigones, and wingless gemmae with a crenulate margin of slightly and regularly bulging cells that are not protruding angularly (Figs 3–5). The status of the two species is confirmed by the molecular analysis (Fig. 2). The detailed description and illustration of *L. pansa* in Engel and Glenny (2019) is a mixture of *L. pansa* and *L. javanica*. In older herbarium material, the papillae of *L. javanica* may sometimes become somewhat inconspicuous and some authors have described the cuticle as being smooth (e.g. Schiffner 1900; but see Stephani 1901). Schiffner (1898) also suggested that trigones are absent in the type of *L. javanica* ("Trigonis nullis"), but we observed distinct trigones in the type material.

3. *Lethocolea naruto-toganensis* Furuki (Furuki 2001: 306)

Type. JAPAN – **Honshu** • Chiba Prefecture, Naruto-machi, Naruto-Togane swamp, on wet sandy soil; ca 5 m; 2 Dec. 1994; *Furuki 11806*; holotype: CBM not seen.

Illustration. Furuki (2001: fig. 1).

Brief description (after Furuki 2001). Plants paroicous, green to brownish-green, small, up to 1 cm long and 2 mm wide, with ventral stolons. Stems ventral surface green (?). Rhizoids purple-red, rarely hyaline. Leaves imbricate, ovate, 1.0–1.5 mm long and wide. Leaf cells rather large, 50–75 × 30–50 μm in midleaf, thin-walled, without trigones; cuticle smooth; oil bodies colourless, oblong, 7.5–20 × 7.5–10 μm, minutely granular, with 1–3 pupils ("eye spots"). Androecia bracts similar to leaves, not bulging; antheridia one per bract, positioned near the dorsal edge of the bract, stalk biseriate. Gynoecia terminal, bracts slightly larger than vegetative leaves. Marsupia up to 3 mm long, 0.5–0.7 mm wide, surface hairy, archegonia near the bottom of the marsupium. Sporophytes not observed. Gemmae positioned on the base of dorsal leaf margin near the stem apex, large, 15–20 cells across (0.3–0.5 mm), with a short, 1-celled stalk, biconvex, margin 1–2-stratose, crenulate, made of swollen cells, wing absent. Gemmalings originating from the margins of the gemmae.

Distribution. Only known from the type locality in Japan (Central Honshu).

Habitat. According to Furuki (2001), the plants grow on sandy lowlands along a river surrounded by rice fields and the soils are wet during the agricultural season but dry up during winter. As a consequence, the species dries up and disappears during the winter period. The habitat of the species is unusual and the only one of its kind remaining in Japan, other similar sites having been destroyed by land development. The locality is therefore preserved as a nature reserve by the Japanese government.

Notes. *Lethocolea naruto-toganensis* is the only paroicous species in the genus; the type has not been seen and the description is based on Furuki (2001). In addition to its sexuality, the species stands out by having colourless oil

bodies with 1–3 pupils ("eye spots"), purple-red rhizoids, relatively short marsupia, up to 3 mm long, and large, wingless gemmae, which originate from the bases of dorsal leaf margins, possessing a 1-celled stalk and germinating at the gemma margins. Because of its smooth cuticle and large wingless gemmae, *L. naruto-toganensis* resembles *L. pansa*, but the latter species is dioicous and has hyaline rhizoids, greyish-brown oil bodies and much longer marsupia, up to 10 mm long. Moreover, the gemmalings of *L. pansa* originate from the centre of the gemmae. The possible presence of a gemma stalk, observed in *L. naruto-toganensis* (Furuki 2001), deserves study in *L. javanica* and *L. pansa*.

II. *Lethocolea* subgen. ***Symphyomitra*** (Spruce) Grolle (Grolle 1972: 549)

Symphyomitra Spruce (Spruce 1885: 503).

Neoprasanthus S.Winkl. (Winkler 1969: 69) – Type species: *Neoprasanthus granatensis* S.Winkl. (= *Lethocolea congesta* (Lehm.) S.W.Arnell).

Lethocolea sect. *Pachycolea* R.M.Schust. (Schuster 2021: 531) – Type species: *Lethocolea glossophylla* (Spruce) Grolle (= *L. congesta* (Lehm.) S.W.Arnell).

Type species. *Symphyomitra glossophylla* Spruce (= *L. congesta* (Lehm.) S.W.Arnell).

Description. Stems ventral surface green to brownish-green, stolons present or absent. Leaf cells with a densely papillose cuticle; oil bodies 1–3 per cell (usually 2), dark brown, often persistent in plants with distinct trigones (Fig. 3G, H), ellipsoid to fusiform, 8–10 × 15–25 µm, brown, finely papillose, pupils ("eye spots") absent. Antheridia 1(–6) per bract. Marsupia short-cylindrical, up to 3 mm long, wall 5–6 cells thick, marsupial canal lined by few papilliform cells (Grolle 1972). Capsules splitting to the base into 2–4 valves, with two adjacent valves sometimes remaining partially connate. Asexual reproduction by disciform gemmae absent.

Distribution. One species in Africa, Central and South America, and on the south Atlantic Islands.

4. *Lethocolea congesta* (Lehm.) S.W.Arnell (Arnell 1955: 311)

Figs 1, 3, 6–9

Jungermannia congesta Lehm. (Lehmann 1829: 365) – Type: same as for *Lethocolea congesta*.

Jungermannia radicosa Lehm. & Lindenb. (Lehmann 1834: 35), **syn. nov.** – Type: CHILE • s.loc.; *s.coll.*, ex hb. Kunze; lectotype (designated by Grolle 1965): S [B28853]; isolectotypes: G [G00065222], JE, S [B28852], W.

Lethocolea radicosa (Lehm. & Lindenb.) Grolle (Grolle 1965: 83) – Type: same as for *Jungermannia radicosa*.

Gymnanthe bustillosii Mont. (Montagne 1845: 346) – Type: CHILE – **Valparaiso** • Puerto San Antonio; *Gay s.n.*; lectotype (**designated here**): PC [PC0103210]; isolectotypes: G [G00051870], G [G00051871], PC [PC0770901], PC [PC0770902], PC [PC0770903], PC [PC0770904].

Lethocolea bustillosii (Mont.) Mitt. (Mitten 1876: 64) – Type: same as for *Gymnanthe bustillosii*.

Lethocolea prostrata Mitt. (Mitten 1876: 64) – Type: TRISTAN DA CUNHA • s.loc.; 1873; *Moseley s.n.*; lectotype (**designated here**): NY; isolectotype: G [G0051868].

Symphyomitra prostrata (Mitt.) Steph. (Stephani 1901: 1125) – Type: same as for *Lethocolea prostrata*.

Calypogeia fistulata Mitt. (Mitten 1884: 85) – Type: CHILE – **Juan Fernandez Islands** • s.loc.; *Saunders s.n.*; holotype: NY not seen (syn. fide Grolle 1965).

Calypogeia euthemona Spruce (Spruce 1885: 449) – Type: ECUADOR – **Tunguragua** • Baños; *Spruce s.n.*; lectotype (**designated here**): MANCH; isolectotype: G [G00282600].

Gongylanthus euthemonus (Spruce) Steph. (Stephani 1906: 387) – Type: same as for *Calypogeia euthemona*.

Symphyomitra glossophylla Spruce (Spruce 1885: 503), **syn. nov.** – Type: ECUADOR – **Pichincha** • Nono, "in rupibus montis Pichincha umbrosis humectatis supra pagum *Nono*, alt. 3000 m"; Aug. 1858; *Spruce s.n.*; lectotype (**designated here**): MANCH [cc4628]; isolectotype: G [G00051869].

Lethocolea glossophylla (Spruce) Grolle (Grolle 1965: 83) – Type: same as for *Symphyomitra glossophylla*.

(?) *Symphyomitra glossophylla* Spruce var. *latifolia* Spruce (Spruce 1885: 504) – Type: ECUADOR – **Tunguragua** • "ad terram in umbrosis"; *Spruce s.n.*; type not found (not in MANCH).

Calypogeia solitaria Kaal. (Kaalaas 1911: 96) – Type: CROZET ISLANDS – **East Island** • 60 m; *Ring & Raknes s.n.*; holotype: O not seen (syn. fide Grolle 1965).

Jamesoniella ligulifolia Steph. (Stephani 1911: 18) – Type: CHILE • Patagonia australis, Skyring; 1908; *Halle & Skottsberg 43*; lectotype (**designated here**): G [G000069825]; isolectotypes: S [B24755], S [B24756].

Tylimanthus hallei Steph. (Stephani 1911: 24). – Type: FALKLAND ISLANDS • West Point; 1907; *Halle & Skottsberg 206*; holotype: G [G00128103]; Material of *T. hallei* in S collected by Halle & Skottsberg and labelled "isotype" has a different collection number (363).

Tylimanthus halleanus Steph. (Stephani 1922: 247) – Type: same as for *Tylimanthus hallei*.

Jamesoniella boliviana Steph. (Stephani 1916: 183) – Type: BOLIVIA – **Cochabamba** • Cerros de Malaga; 1910–1911; *Herzog 4411/a*; lectotype (**designated here**): G [G00128139]; isolectotype: JE.

Symphyomitra africana Steph. (Stephani 1917: 102) – Type: TANZANIA • Mt. Kilimanjaro, "Lumifluß"; 3000 m; *H. Meyer 157*; holotype: G [G00067905].

Neoprasanthus granatensis S.Winkl. (Winkler 1969: 69) – Type: COLOMBIA – **Magdalena / Cesar** • "Südflanke der Sierra Nevada de Santa Marta, Tal von Duriameina"; 3300 m; 1967; *Winkler C395a*; holotype: ULM not seen (syn. fide Grolle 1972).

(?) *Symphyomitra tabularis* S.W.Arnell (Arnell 1953: 114) – Type: SOUTH AFRICA – **Western Cape Province** • Hottentots-Holland Mountains, Steenbrass River mouth; 1951; *Arnell 694*; lectotype (**designated here**): S ["Material present in the herbarium, but no specimens have yet been registered in the database"] not seen (syn. fide Arnell 1955). As explained below, the type of *S. tabularis* belongs to *L. congesta* or *L. pansa*.

Type. SOUTH AFRICA – **Western Cape Province** • Tafelberg; *Ecklon s.n.*; lectotype (**designated here**): S [B25217]; isolectotypes: S [B25218], S [B25221], S [B25222], G [G00115872], G [G00115873], G [G00115874], JE, W [2010-01828].

Description. Plants dioicous, 1–2 cm long, 1–3(–4) mm wide, creeping or ascending, dull, pale to rather dark green to yellowish-green to yellowish-brown, becoming more pale-coloured and transparent on older shoot portions; branching ventral-intercalary and stoloniform or (rarely) lateral-intercalary and leafy, stolons usually near the base of the stem, occasionally higher up the stem and sometimes originating from below the immature marsupium. Stems fragile to rigid, colourless or pale green to brownish-green (never purplish-reddish), 0.25–0.5 mm in diameter, made up of 190–290 thin-walled cells. Rhizoids scattered or slightly fascicled, hyaline to light brown. Leaves present throughout the stem or limited to the upper portion of stem (the lower portion of stem thus stoloniform), green or occasionally tinged purple or red, densely imbricate and upright when growing exposed, more loosely imbricate or distant and spreading when growing in shade, towards the shoot apex usually upright and appressed, obliquely to widely spreading on older stem portion, suborbicular to ovate-oblong to oblong to lingulate, widest at 1/3–1/2 of leaf length, 0.8–2.1 mm long, 0.8–1.4 mm wide, 1–2.2× longer than wide, flat in upper half and concave-convex in the lower half, apex usually rounded, occasionally truncate to emarginate, dorsal margin straight or slightly narrowed to the base, ventral margin arched and slightly to distinctly narrowed to the base, dorsal base shortly to moderately decurrent, ventral base not decurrent, lamina more transparent in the lower ventral half of the leaf due to larger cells with little or no chlorophyll. Cells in midleaf isodiametric-hexagonal to slightly elongate, 25–50(–60) × 20–40 μm, at the leaf margin slightly smaller and quadrate to rectangular, thin-walled, sometimes thick-walled and forming a border in plants with conspicuous trigones; cells in the lower ventral half of the leaf more hyaline, enlarged and elongate, about 2–4× longer than wide, 40–100 × 20–40 μm, becoming gradually narrower and more elongate towards the margin, to 6× longer than wide, 2–10 cell rows along the lower ventral margin without chlorophyll and in part lacking oil bodies, enlarged hyaline cells may extend high up in the ventral half of the leaf and sometimes in the upper half to near the apex (in plants from dry, Mediterranean environments); cuticle papillose both dorsally and ventrally, papillae colourless, rounded to suboblong, 2–5(–10) × 2–3(–8) μm, becoming more elongate to linear on the cells in the lower ventral half of the leaf; cell walls with minute to large trigones, the trigones to 10 μm in diameter, with concave to slightly bulging walls, not confluent (except sometimes on short cell walls); oil bodies 1–3 per cell, dark brown, persistent in rather rigid plants with distinct trigones (seen in up to 100 years old herbarium specimens), vanishing in flaccid plants with minute trigones, ellipsoid to fusiform, 2–3× longer than wide, 8–10 × 15–25 μm, finely granular. Androecia terminal or intercalary, bracts in (1–)3–20 pairs, rather similar to vegetative leaves but more deeply pouched towards the base and with dorsal margin incurved; antheridia 1(–6) per bract. Gynoecia terminal on a main shoot, when unfertilized often with a ventral branch, bracts as large as or slightly larger than vegetative leaves, usually upright and appressed, in gynoecia with mature marsupia sometimes slightly spreading outwards. Marsupia conical-subcylindrical, green when young, brown when mature and with a hairy surface, up to 3 mm long, 2.5–3× longer than wide, tapered towards the tip (tip not swollen). Sporophytes foot embedded inside the marsupium, elongated seta and capsule long-exserted; seta whitish, up to 1.2 cm long after elongation, formed by ca 70 cell rows, cells isodiametrical to somewhat elongate, with small trigones, the trigones of outer cell walls more conspicuous; capsule (before dehiscence) dark brown, cylindrical, tip apiculate, with four dehiscence lines, upon dehiscence splitting to the base into four valves or into only 2–3 valves with two adjacent valves remaining partially connate, valves erect, 1.5–3.0 × 0.7–1.0 mm, wall 2(–4)-stratose, being mostly 2-stratose with limited 3–4-stratose areas (Fig. 9F), cells of the outer layer quadrate to long-rectangular, 37–100 × 18–32 μm, walls thin but firm, yellowish to reddish-brown, with small, orange to reddish-brown, nodular thickenings evenly spaced along the longitudinal walls, turning into conspicuous thickening bands on radial walls, cells of the inner layers variable in shape and size, trapezoidal-elongate, rounded-rectangular to rounded-quadrate, 37–85 × 28–40 μm, walls thin, hyaline, without thickenings; elaters with 1–2 spirals, narrowly fusiform, 130–200 × ca 10 μm, narrowed toward the tips, the tips rounded, surface finely punctate; spores (from herbarium material soaked in water) isodiametrical, ca 25 μm in diameter, yellowish to brown, spore surface finely papillose. Gemmae absent.

Distribution. In high mountain areas of tropical America (Mexico to Bolivia, southeastern Brazil, Dominican Republic) and tropical Africa (Central and East Africa, Réunion), furthermore in Mediterranean and temperate areas of southern South America (especially Chile), on the south Atlantic Islands (Tristan da Cunha, Prince Edwards Is., Crozet Is.), and in South Africa.

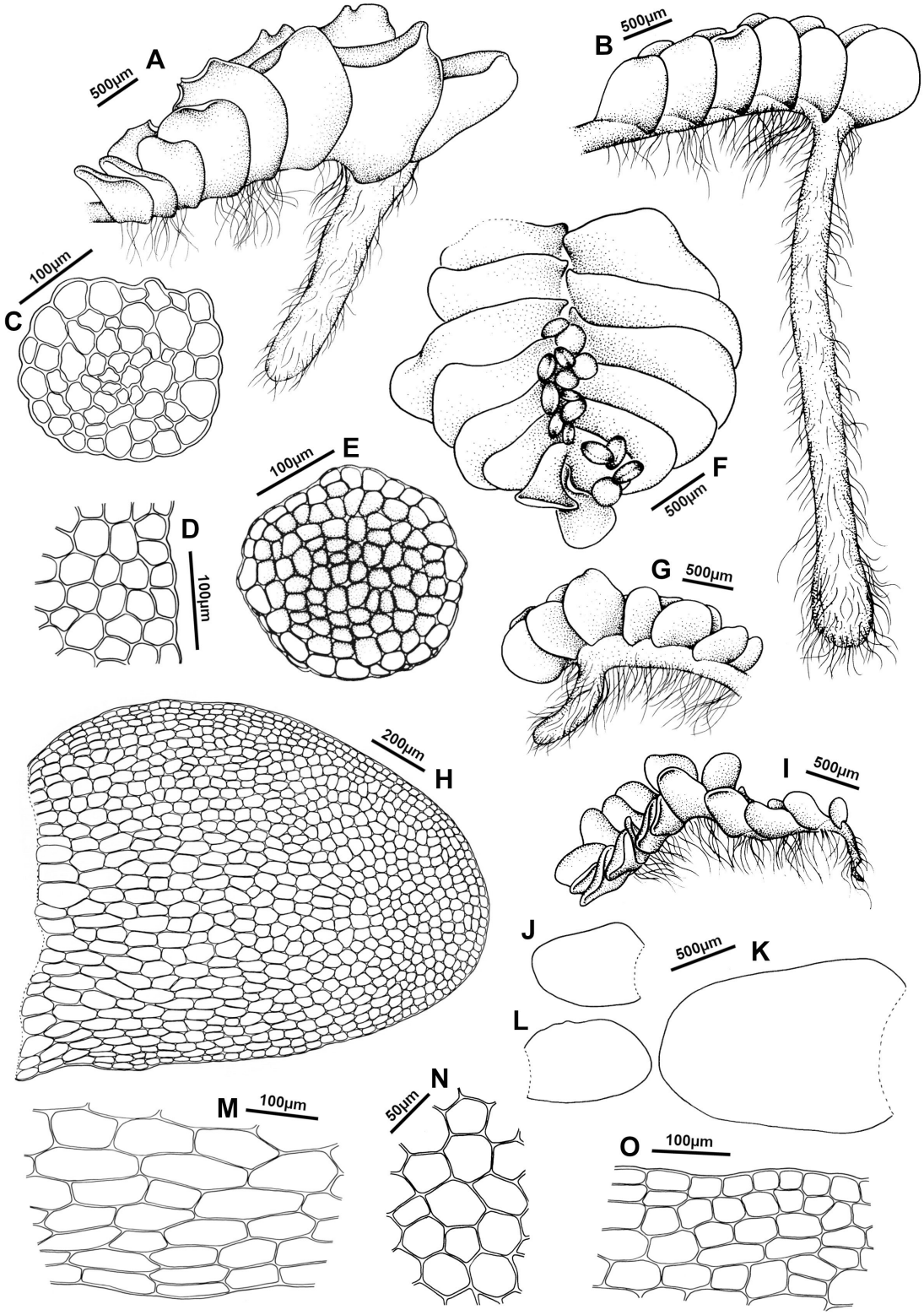

Figure 6. *Lethocolea pansa*. **A**, **G**. Female shoot with immature marsupium. **B**. Female shoot with mature marsupium. **C**. Cross section of stem. **D**. Cells at leaf apex. **E**. Gemma. **F**. Portion of shoot with gemmae, dorsal view. **H**, **J**–**L**. Leaves. **I**. Sterile shoot. **M**. Cells at ventral leaf base. **N**. Midleaf cells. **O**. Cells at dorsal leaf base. A, C–E, G–I, M–O from *Esterhuysen 27343*; B, L from *Hedderson 152686*; F, J–K from *Arts 129/11*. Drawn by Anna Luiza Ilkiu-Borges.

Habitat. *Lethocolea congesta* grows on moist soil along trails, on earth banks, and near rivulets, as well as on soil over acidic and lava rock, exceptionally on tree bases. In tropical regions, the species occurs in montane and subalpine forest areas and páramó, at (1000–)2000–4500 m, in Mediterranean and temperate regions in scrubby

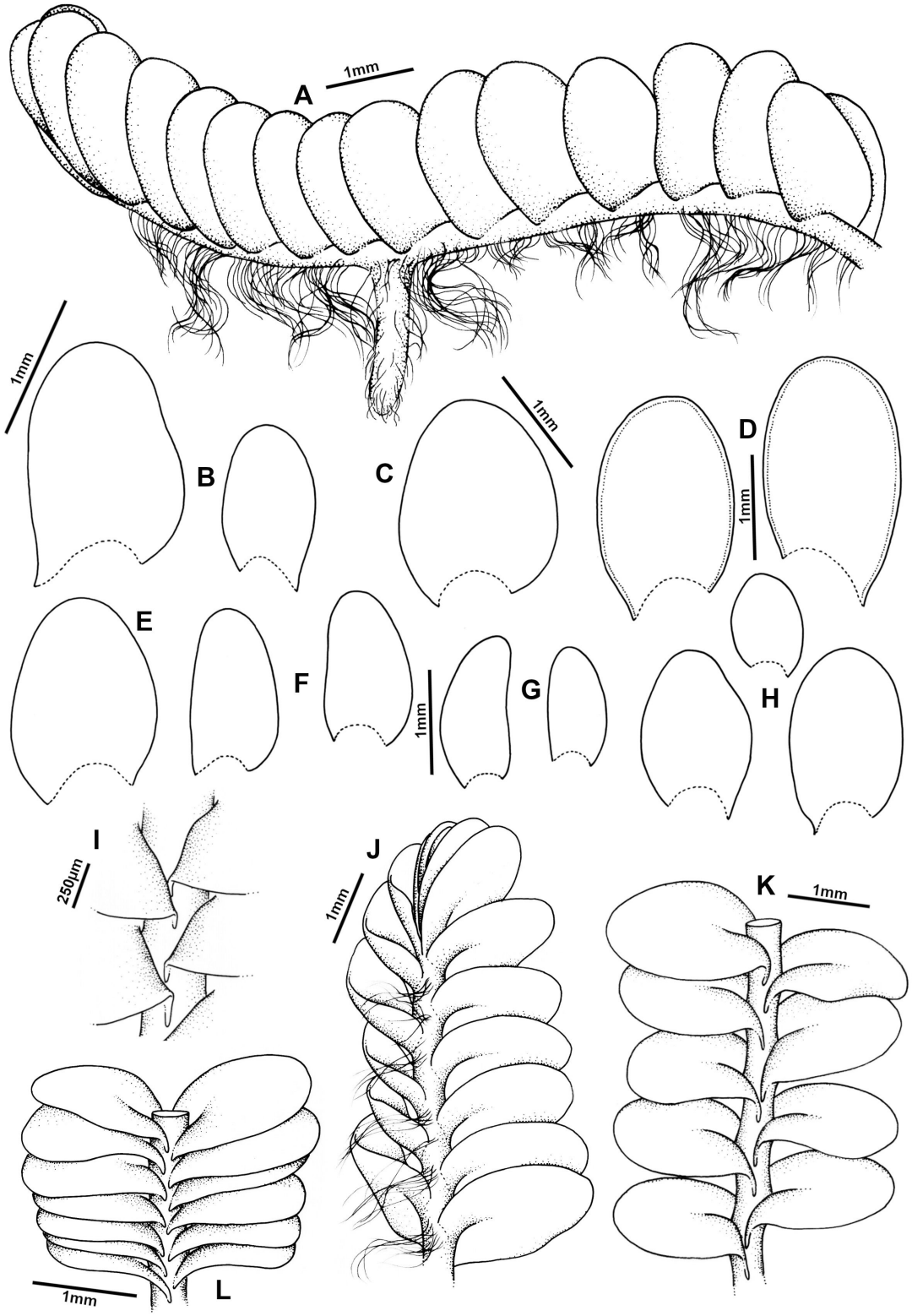

Figure 7. *Lethocolea congesta.* **A**. Shoot. **B**–**H**. Leaves. **I**. Leaf insertion, dorsal view. **J**. Shoot, ventral view. **K**–**L**. Shoot, dorsal view. A, D, J–K from *Holz 209*; B from *Gradstein 10165*; C, E from *Arts 129/02*; F–G, L from *Arts 19/54*; H–I from *Larrain 42566*. Drawn by Anna Luiza Ilkiu-Borges.

vegetation, often rather xerophytic, from sea level to 1000 m.

Additional material examined. MEXICO – **Mexico** • Passo Puerto de la Cruces; 3000 m; *Düll 21332*; JE.

COSTA RICA – **Cartago** • Cordillera de Talamanca, near Panamerican highway; 3350 m; *van Melick 214515*; PC • Chirripó; 3550 m; *Kuhbier 627*; JE • Páramo Buena Vista; 3250 m; *Holz CR2009*; GOET.

VENEZUELA – **Mérida** • Páramo de Mucuché; 3300–3700 m; c. gyn.; *Griffin PV395*; GOET • Páramo de Mucubaji; 3500–3600 m; *Drehwald 40133*; GOET.

COLOMBIA – **Boyacá** • Sierra Nevada del Cocuy, Corralitos; 3900 m; c. gyn.; *Bischler 2881*; G, PC • same data as for preceding; 4000 m; *Bischler 2997*; G, PC • Sierra Nevada del Cocuy, near laguna La Pintada; 4300–4700 m; *Bischler 2829*; PC. – **Caldas** • Nevado del Ruiz; 4200 m; *Bischler 291*; G, PC • same data as for preceding; 3780 m; c. gyn.; *Florschütz 4396*; GOET • ibid., near hotel Termales; 3460 m; *Cleef 2386*; GOET. – **Cauca** • Páramo de las Papas; 3200–3600 m; *Bischler 918*; GOET. – **Cundinamarca** • Páramo de Chingaza; 3460 m; c. gyn. & andr.; *Gradstein 4249*; GOET. – **Risaralda** • Parque de los Nevados, Páramo de Santa Rosa; *Aguirre et al. 4875*; GOET • same data as for preceding; *Aguirre et al. 4952*; GOET.

ECUADOR – **Carchi** • Páramo El Angel; 3400 m; c. andr.; *Arts 14/067*; QCA • same data as for preceding; 3300–3630 m; *Gradstein et al. 3349*; GOET • same data as for preceding; *Gradstein et al. 6834;* GOET. – **Cotopaxi** • Parque Nacional Llanganates, vicinity of Laguna Anteojos; 4000 m; *Burghardt et al. MB6806*; PC • Near Sindipamba; c. gyn.; *Arts 23/005c*; JE • Cotopaxi National Park, along road near the Park entrance; 3550 m; *Gradstein & Frahm 6667*; GOET. – **Pichincha** • Road Lloa – Río Cristal; *Gradstein & Frahm 6698*; G, GOET • Old road Quito to St. Domingo, W of San Juan; ca 3000 m; *Gradstein et al. 6720*; GOET • Quito, Parque Metropolitano; 2800 m; *Burghardt 6555*; QCA. – **Zamora-Chinchipe** • Podocarpus Nat. Park, Río Bombuscara; 1000 m; *Schäfer-Verwimp & Preussing 23417*; GOET.

PERU – **Apurimac** • Huancaras; 3700 m; c. marsup.; *Hegewald 5708*; JE. – **La Libertad** • Road to Otuzco, near Esquil; leaves bordered; *Hegewald 7197*; JE.

BOLIVIA • Torreni-Yamakaka; ca 4500 m; leaves partially bordered; *Herzog 3739*; JE. – **Cochabamba** • Incachaca; 3400 m; *Gradstein 7397*; GOET. – **Santa Cruz** • Near Vallegrande; 2500 m; *Churchill 22308*; MO, GOET.

CHILE – **Juan Fernandez Islands** • Masafuera; ca 400 m; *Hatcher & Engel 48*; JE. – **Coquimbo** • Fray Jorge; *Schwabe 227*; JE. – **Valparaíso** • Nature Reserve La

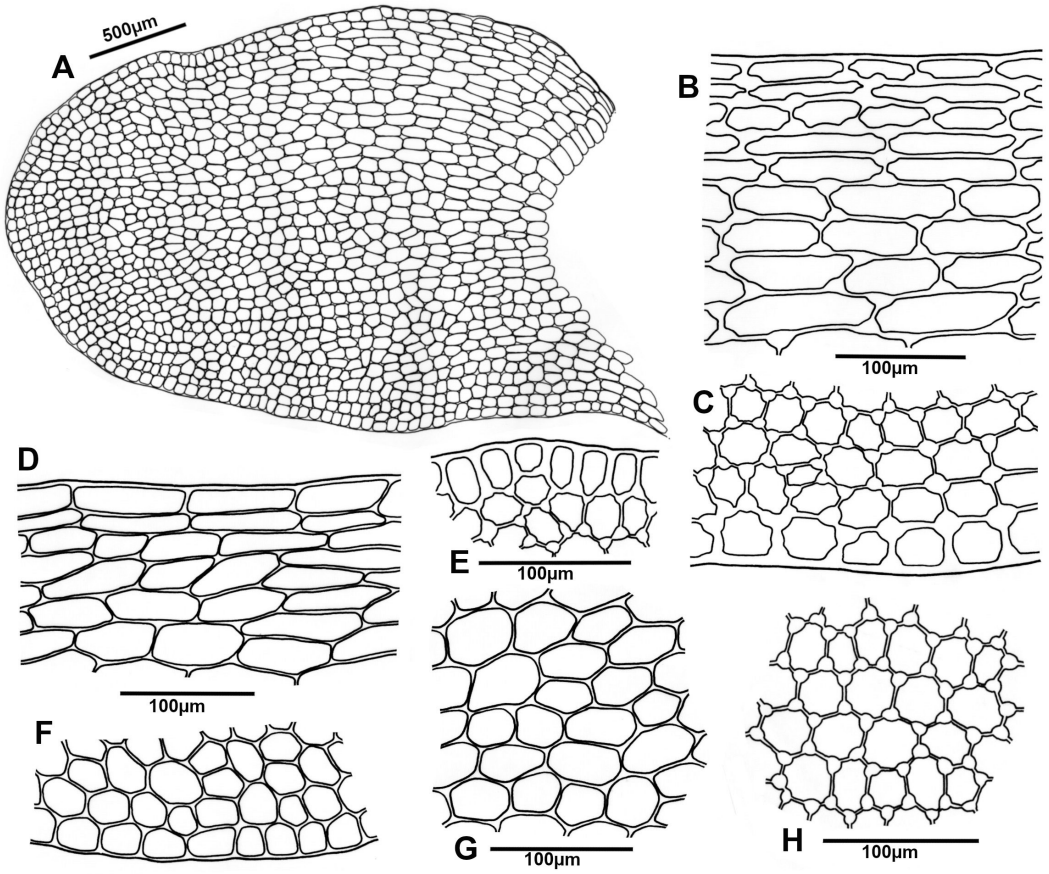

Figure 8. *Lethocolea congesta.* **A**. Leaf. **B**. Margin cells near ventral leaf base, showing border. **C**. Margin cells near dorsal leaf base, showing border. **D**. Margin cells near ventral leaf base. **E**. Margin cells at leaf apex. **F**. Margin cells near dorsal leaf base. **G**. Midleaf cells. **H**. Midleaf cells. A, F–G from *Gradstein 10165*; B from *Holz 209*; C–E, H from *Arts 129/02*. Drawn by Anna Luiza Ilkiu-Borges.

Campana; ca 500 m; *Gradstein & Cuvertino 12426-B*; PC • same data as for preceding; *Larrain 43934*; BR • same data as for preceding; *Larrain 43937*; BR • La Ligua; 458 m; *Larrain 45507*; BR • Viña del Mar; *Larrain 40415*; BR • Laguna Peñuelas; 380 m; *Mahu 13006*; JE, MO, PC • El Tabo; 20 m; *Mahu 11862*; JE. – **Metropolitana** • Reserva Altos de Cantillana; 1869 m; *Larrain 43526*; BR • Laguna de Aculeo; *Mahu 21984*; JE. – **Libertador** • Sierras de Bellavista; 1600 m; *Mahu 20139*; JE, MO. – **Maule** • Talca; 1230 m; *Mahu 50004*; MO • Talca; 1230 m; *Mahu 50060*; MO • Linares; 764 m; *Larrain 42566*; BR. – **Nuble** • San Fabian; between *Leptoscyphus expansus*; 250 m; *Mahu 9310*; MO. – **Araucanía** • Cerro Lungoico, 1000 m, *Schwabe 109*; JE • Pucón; *Mahu 11501*; JE, MO • Volcán Villarica; *Hosseus 211*; JE. – **Los Ríos** • Corrál; 10 m; *Mahu 13559*; JE • Niebla; 30 m; *Mahu 12007*; JE. – **Los Lagos** • Llanguihue, Yerbas Buenas, near Area de Recreación Las Cascadas; 20 m; c. marsup.; *Mahu 21410*; MO • same date as for preceding; 20 m; c. marsup.; *Mahu 21438*; MO. – **Chiloë** • Quicavi; c. marsup. & spor.; *Halle 139*; JE. – **Tierra del Fuego** • Isla Grande, Cerro Recalada; *Hyvönen 32212*; JE.

ARGENTINA – **Chubut** • Parque Nacional Los Alerces, Alerzal; 560 m; *Hyvönen 5502a*; JE.

DEMOCRATIC REPUBLIC OF CONGO – **Lacs Edouard et Kivu** • Mt. Karisimbi; 3400 m; *De Sloover 13131*; BR [BR5040101618594] • same data as for preceding; *De Sloover 13150*; BR [BR5040264975688].

RWANDA – **Lacs Edouard et Kivu** • Mt. Muhavura; ca 3900 m; *De Sloover 13634*; BR [BR5040264976692] • Mt. Karisimbi, *Hagenia* forest; *Frahm 8048*; G.

UGANDA • Kigezi; c. gyn. & andr.; *Hedberg 2156;* BR [BR5040101615562] • Ruwenzori, Lac Mahoma; 3050 m; *Lisowski 2984*; BR [BR5040034019697].

KENYA • Mt. Kenya, NW slopes; 3450 m; *Hedberg 1990a*; JE • Moru track; 3800 m; *Agnew 345*; JE.

TANZANIA • Mt. Kilimanjaro, Makoa River below Machame hut; 2960 m; *Pócs 6976/AH*; G • ibid., trail Madara hut to Horombo hut; 3400 m; *Albertshofer s.n.*; JE • ibid., Shira Plateau; 4000 m; *Lewinsky B627*; BR [BR5040264971642] • South Uluguru Mts, gorge of Mgeta River; 2215–2370 m; *Pócs 6829/J*; G, JE, PC • Mt. Meru, Engare Narok gorge; 2490 m; *Pócs & Kis 9145/A*; GOET.

RÉUNION • Plaine des Cafres; 1570–1600 m; *Onraedt 74R8378*; JE • Sentier de Langevin; 2100 m; *Onraedt 71R7573*; BR [BR5040235549337]; JE • Forêt du Taibit; ca 2000 m; leaves bordered; *Onraedt 74.R.8687*; JE • Forêt du Taibit; 1750 m; leaves bordered; *Onraedt 75R942*; BR [BR5040235558421] • Footpath to La Nouvelle; 1610 m; *Arts 61/69*; BR [BR5040315946179] • Cirque de Cilaos; 1600 m; leaves bordered; *Onraedt 73R1229*; BR [BR5040235550340] • Sentier vers Piton des Neiges; 1550 m; leaves bordered; *Arts 19/54*; BR [BR5040315939102] • same data as for preceding; 2000 m; c. marsup.; *Onraedt 70R4530*; JE • Trail to Piton de la Fournaise, Pas de Bellecombe; *Onraedt 69R330*; BR [BR5040101616576], JE • Pas des Sables, between Bourg Murat and Piton de la Fournaise; 2320 m; *Arts 42/04*; BR [BR5040315941129].

SOUTH AFRICA – **Natal** • Drakensberg Gardens, near Wilson's Cave; *Meyer 1052c*; GOET • Bergville Division, Drakensberg, Injasuti area; 5000–9000 ft.; *Esterhuysen 26104*; BOL • ibid., Ndederna area; 6000 ft.; *Esterhuysen 22986*; BOL. – **Western Cape Province** • W of Cape Town, NW slope of Devils Peak; 300–400 m; *Rolfe 81*; JE • Constantia slopes; leaves bordered; *Arnell 375*; BOL • Jeep track from Constantia Neck to Table Mountain; 300–700 m; leaves bordered; *Arts 129/02*; BR [BR5040313690890] • same data as for preceding; *Arts 129/43*; BR [BR5040313688873] • Kasteel Poort; *Arnell 1103*; JE • Between Kloof Nek and Brinkwater Ravine; *Arnell 1104*, paratype of *Symphyomitra tabularis*; BOL [BOL0233665] • Kirstenbosch & Kloof Nek; *Bottomley 212*, as *Odontoschisma sphagni*; PRE, S • Kirstenbosch; *Esterhuysen 2*; BOL • same data as for preceding; *Vanden Berghen s.n.*; BR [BR5040034017679] • Camps Bay; *Garside 6681*; BOL • Ceres Division, Hansiesberg; ca 1250 m; *Esterhuysen 25689*; BOL.

Notes. *Lethocolea congesta* is a widely distributed and highly variable, Afro-American species that has been described under many different names. In tropical America, the species was known as *L. glossophylla* and in southern South America and on the south Atlantic Islands as *L. radicosa*. Both appear to be synonyms of *L. congesta*. *Lethocolea congesta* differs from the other members of the genus in having 1–3 (usually 2) dark brown oil bodies per cell (Fig. 3G, H) and in lacking asexual reproduction by disciform gemmae. Moreover, the marsupia are shorter, maximally 3 mm long and conical-subcylindrical in shape (Fig. 9A, C, E), and the marsupial canal is lined by few papilliform cells.

The leaves in *Lethocolea congesta* range from suborbicular to ovate-oblong to narrowly lingulate and the area of enlarged, hyaline cells in the ventral half of the leaf may be restricted to the base or extending upwards, exceptionally to near the leaf apex. The hyaline area in the leaf is usually more extensive in Mediterranean plants from low elevation than in the plants from high elevation in the Tropics. The cuticle of the leaf cells is densely papillose, although the crowding of the papillae may vary somewhat (Fig. 3A, D), and the trigones may be very small, ca 1 mm in diameter, or well-developed, up to 10 µm in diameter (Fig. 8G, H). The size of the trigones seems to correlate with elevation as well and is usually smaller in plants from low elevation than from high elevation. The latter plants are usually more rigid (and easier to dissect) than those from low elevation and herbarium specimens from high elevation often had well-preserved oil bodies (Fig. 3G, H), which were found intact in up to one hundred years old dried material. In herbarium specimens from low elevation, in contrast, oil bodies had usually vanished.

The thickening of the walls of the leaf margin cells is normally similar to that of the inner leaf cells (Fig. 8D, F). In some specimens, however, they were thicker-walled (by confluent trigones) than the inner cells, forming a thickened border extending along part of, or almost the entire leaf margin (Fig. 8B, C). Leaf borders

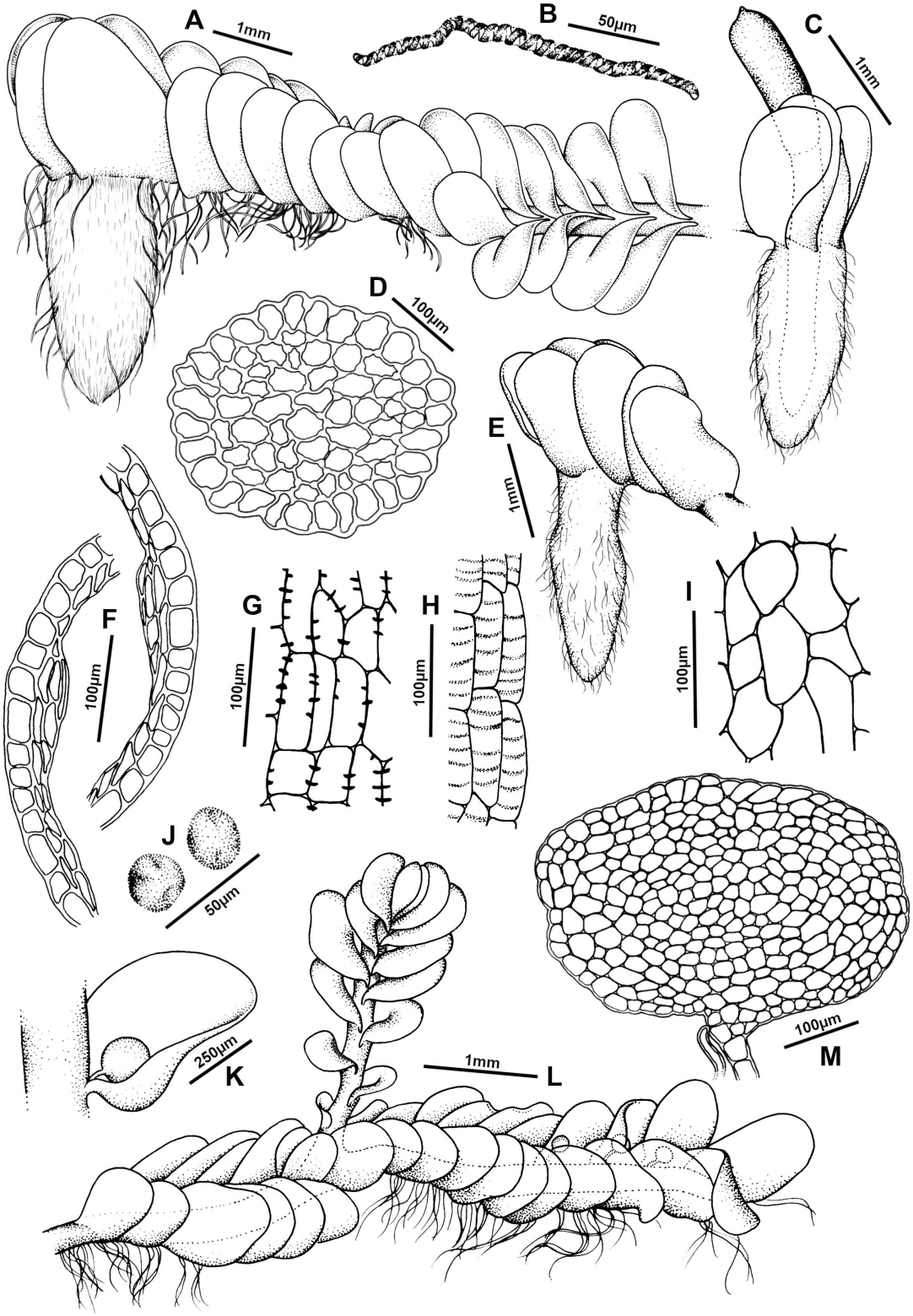

Figure 9. *Lethocolea congesta*. **A**, **E**. Female shoot with near-mature marsupium. **B**. Elater. **C**. Shoot apex with mature marsupium, female bracts and mature sporophyte before dehiscence, showing apiculate capsule. **D**. Cross section of seta. **F**. Cross sections of capsule. **G**. Outer cells of capsule wall, frontal view. **H**. Outer cells of capsule wall, lateral view. **I**. Inner cells of capsule wall, frontal view. **J**. Spores. **K**. Male bract with antheridium. **L**. Male plant with androecia. **M**. Cross section of stem. A from *Onraedt 70.R.4539*; B–J from *Halle 139*; K–L from *Larrain 45507*; M from *Holz 209*. Drawn by Anna Luiza Ilkiu-Borges.

of thick-walled cells occur in several genera of liverworts, e.g. in *Adelanthus* Mitt., *Bazzania* Gray, *Calypogeia* Raddi, *Odontoschisma* (Dumort.) Dumort., *Plagiochila* (Dumort.) Dumort., *Scapania* (Dumort.) Dumort., and *Radula* Dumort., and can be a useful and stable taxonomic character to distinguish species (Oliveira da Silva et al. 2022). In *L. congesta*, however, the development of a border – seen in specimens from throughout the range of the species – was variable and appeared to be without taxonomic relevance as no correlation with other characters was observed.

Young gynoecia with very short, bulging marsupia were not uncommon and were most frequently seen in plants from exposed sites. The female bracts are normally upright and tightly appressed, but in in gynoecia with fully grown marsupia they were sometimes spreading outwards. One or two innovations may sprout from the bulging base of young gynoecia. Mature marsupia and sporophytes are rare and were only seen in two old collections from Chile, i.e. Valparaiso, *Gay s.n.* (type of *Gymnanthe bustillosii* Mont.) and Chiloë I., *Halle 139* (Fig. 9B–I). Spruce (1885) provided a detailed description of the mature marsupium and sporophyte in *L. glossophylla* based on the type collection from Ecuador. However, plants with marsupia could not be found in the type material of *L. glossophylla* kept in the Spruce herbarium (MANCH). A peculiar feature of the capsule of *L. congesta* is that dehiscence is sometimes incomplete, with capsules splitting to the base into only 2–3 valves (instead of 4 valves) with two adjacent valves remaining partially connate.

Male plants were less frequent than female plants. The length of the male spikes appeared to be highly variable, of 1–20 consecutive pairs. In a few instances male and female plants were found growing mixed (e.g. Uganda, *Hedberg 2156*; Colombia, *Gradstein 4249*); nevertheless, no sporophytes were observed in these specimens.

Several authors have suggested the occurrence of gemmae in African *Lethocolea congesta* (e.g. Arnell 1963; Grolle 1969; Gradstein et al. 1983; Schuster 2021). These reports are erroneous and were based on Arnell (1963) who included gemmiferous plants belonging to *L. pansa* in his treatment of *L. congesta* (this study). It has also been suggested that *L. congesta* is paroicous (based, again, on Arnell (1963) who wrote "Paroicous?"), but no paroicous plants of *L. congesta* have been seen in this study.

In the Neotropics, *L. congesta* has been confused with *Solenostoma amplexifolium*, but the latter species has a smooth cuticle and also lacks an area of elongated, hyaline leaf cells. Moreover, the rhizoids in *S. amplexifolium* are usually reddish or brown (rarely hyaline), the leaves are concave with the dorsal base clasping the stem (rarely plane, e.g. Mexico, *Burghardt 4495*, identified as *L. glossophylla*), and the oil bodies are colourless and not persistent.

Stephani (1906: 222) erroneously placed *Lethocolea congesta* in synonymy of *Leptoscyphus expansus* (Lehm.) Grolle. The latter species often grows mixed with *L. congesta* in Chile and South Africa, on earth banks, and superficially resembles *L. congesta* in habit. The presence of underleaves with rhizoids sprouting in bundles from underleaf bases, and the absence of an area of elongated hyaline cells in the lower ventral half of the leaf clearly separate sterile material of *Leptoscyphus expansus* from *L. congesta*.

Symphyomitra tabularis is tentatively placed here in synonymy of *L. congesta* following Arnell (1955, 1963). The synonymy needs verification as the original description of *S. tabularis* (Arnell 1953) was a combination of *L. congesta* and *L. pansa*. The leaves tinged purple, the papillose cuticle, and the presence of 1–3 oil bodies per leaf cell mentioned in the protologue of *S. tabularis* are characters of *L. congesta*, but the disciform, wingless gemmae mentioned in the original description point to *L. pansa*. The description of *S. tabularis* was used almost unaltered in the treatment of *L. congesta* in the South African hepatic Flora (Arnell 1963). We have been unable to study the type of *S. tabularis*, which was deposited in BOL and S (Arnell 1953). The isotype in BOL is apparently missing (Cornelia Klak pers. comm.) and the type material in S – which is present there according to the database of S – is currently unavailable due to the renovation of the Stockholm herbarium. Arnell (1953), additionally, cited four paratype collections, two from Constantia slopes and two from Kasteel Poort. We have examined the two paratype specimens from Kasteel Poort based on duplicates kept in BOL and G; one of them belongs to *L. pansa* (*Arnell 1036*, G), the other is *L. congesta* (*Arnell 1104*, BOL). In addition, numerous non-type specimens have been examined from Constantia slopes, collected by Arnell and others, where *Lethocolea* seems to be common. These collections also included both species. It may thus well be possible that the type of *S. tabularis* belongs to *L. pansa* rather than *L. congesta*.

Doubtful species

Lethocolea indica G.Asthana & Maurya (Asthana and Maurya 2014)

Type. INDIA – **Western Himalaya** • Uttarakhand, Pauri (Garhwal hills); 30°08.462'N, 78°46.920'E; ca 1788 m; 23 Oct. 2010; *Asthana et al. 20985/10*; holotype: LWU not seen • Uttarakhand, Almora (Kumaonhills), 1 km before Petsal; 29°37.1440'N, 79°43.2690'E; ca 1346 m; 23 Mar. 2011; *Maurya 21581/11*; paratype: LWU not seen.

Notes. *Lethocolea indica* is only known from the holotype and paratype. The type material, which was not received on loan, was apparently a mixture of *Lethocolea* and *Jackiella* (Jackiellaceae) as is indicated by the illustrations of the holotype (Asthana and Maurya 2014: figs 1, 2). The depicted disciform gemmae are typically those of *Lethocolea*, although the presence of both broadly winged and wingless ones (Asthana and Maurya 2014: figs 1-16, 2-C) is atypical. The portions of plants shown in dorsal and lateral view do not represent *Lethocolea* and apparently belong to *Jackiella* by the dorsal leaf insertions

not reaching the dorsal midline of stem (Asthana and Maurya 2014: fig. 1-1) and the androecia on short ventral or ventro-lateral branches (Asthana and Maurya 2014: figs 1-2, 1-3).

Excluded names

Lethocolea amplexifolia (Lehm.) Grolle = *Solenostoma amplexifolium* (Lehm.) Váňa & Schäf.-Verw. (Schäfer-Verwimp and Pócs 2009).
Lethocolea concinna (Mitt.) Bastow (*Symphyomitra concinna* (Mitt.) Steph.) = *Acrobolbus concinnus* (Mitt.) Grolle (Grolle 1965).
Lethocolea grandifolia Berggr. = *Solenostoma hodgsoniae* J.J.Engel (Engel and Glenny 2008).
Lethocolea repens S.Winkl. = ? *Gongylanthus liebmannianus* (Lindenb. & Gottsche) Steph. (Gradstein 2021).
Symphyomitra weymouthii Pearson = *Acrobolbus concinnus* (Mitt.) Grolle (Grolle 1965).

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REFERENCES

Alam A (2014) Morphotaxonomy of three rare terricolous taxa of Jungermanniales occurrring in Nilgiri Hills (Western Ghats) India. International Journal of Environment 3: 263–275. https://doi.org/10.3126/ije.v3i2.10640
Arnell S (1953) Hepaticae collected in South Africa 1951. Svensk Botanisk Tidskrift 47: 113–115.
Arnell S (1955) Notes on South African Hepatics II. Botaniska Notiser 108: 309–313.
Arnell S (1963) Hepaticae of South Africa. Swedish Natural Science Research Council, Stockholm, 1–411.
Asthana G, Maurya M (2014) *Lethocolea indica*: a new liverwort from India. National Academy of Science and Letters 37: 535–539. https://doi.org/10.1007/s40009-014-0274-z
Briscoe L, Engel JJ (2016) Acrobolbaceae. In: Söderström L et al. [43 co-authors]. World checklist of hornworts and liverworts. PhytoKeys 59: 93–98. https://doi.org/10.3897/phytokeys.59.6261
Cargill DC (2022) *Riccia epecenia*: a new species of *Riccia* section *Piliferae* Volk from Australia. Bryophyte Diversity & Evolution 45: 85–94. https://doi.org/10.11646/bde.45.1.6
Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B, Flouri T (2020) ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. Molecular Biology and Evolution 37: 291–294. https://doi.org/10.1093/molbev/msz189
Engel JJ, Glenny D (2008) A Flora of the Liverworts and Hornworts of New Zealand, Vol. 1. Monographs in Systematic Botany from the Missouri Botanical Garden 110: 1–898.
Engel JJ, Glenny D (2019) A Flora of the Liverworts and Hornworts of New Zealand, Vol. 3. Monographs in Systematic Botany from the Missouri Botanical Garden 135: 1–636.
Flagmeier M, Draper I, Vigalondo B, Garilleti R, Lara F (2021) So close yet so far: the disjunct global range of *Orthotrichum consobrinum* (Orthotrichaceae) includes North America. The Bryologist 124: 403–413. https://doi.org/10.1639/0007-2745-124.3.403
Furuki T (2001) *Lethocolea naruto-toganensis*, a new hepatic from swamps of Japan. The Bryologist 104: 306–309. https://doi.org/10.1639/0007-2745(2001)104[0306:LNTANH]2.0.CO;2
Galley C, Linder HP (2006) Geographical affinities of the Cape Flora, South Africa. Journal of Biogeography 33: 236–250. https://doi.org/10.1111/j.1365-2699.2005.01376.x
Goebel KI (1906) Archegoniatenstudien. Flora oder Allgemeine Botanische Zeitung 96: 1–202.
Gottsche CM (1880) Neuere Untersuchungen *über* die Jungermannieae Geocalyceae. Abhandlungen des Naturwissenschaftlichen Vereins Hamburg 7: 39–66.
Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution 27: 221–224. https://doi.org/10.1093/molbev/msp259
Gradstein SR (2013) Afro-American hepatics revisited. Polish Botanical Journal 58: 149–177.
Gradstein SR (2021) The liverworts and hornworts of Colombia and Ecuador. Memoirs of the New York Botanical Garden 121: 1–723. https://doi.org/10.1007/978-3-030-49450-6
Gradstein SR (2024) Division B. Marchantiophyta, Partie 1: Haplomitriopsida & Jungermanniopsida: Jungermanniales. In: Sosef MSM (Ed.) Flore d'Afrique centrale, série Bryophytes. Meise Botanic Garden, Meise, 1–172..
Gradstein SR, Váňa J, Pócs T (1983) Disjunct Hepaticae in tropical America and Africa. Acta Botanica Hungarica 29: 127–171.
Grolle R (1965) Über *Gymnanthe concinna* und *Lethocolea*. Botanical Magazine Tokyo 78: 78–84.
Grolle R (1969) Miscellanea hepaticologica 101–110. *Österreichische* Botanische Zeitung 117: 1–6.
Grolle R (1972) Miscellanea hepaticologica 121–130. Journal of the Hattori Botanical Laboratory 36: 547–551.
Hedderson TA (2012) *Bryobartramia schelpei* T.A.Hedderson, a new species to accommodate the South African populations of the genus. Journal of Bryology 34: 257–263. https://doi.org/10.1179/1743282012Y.0000000022
Hodgson EA (1958) New Zealand Hepaticae (Liverworts) X. Marsupial genera of New Zealand. Transactions of the Royal Society of New Zealand 85: 565–584.
Hooker JD (1867) Handbook of the New Zealand Flora 2. Reeve & Co., London, 393–798.
Hürlimann H (1974) Hepaticae aus dem Gebiete der südlichen Pazifik III. Bauhinia 5: 59–68.
Hürlimann H (1985) Hepaticae aus dem Gebiete der südlichen Pazifik VIII. Bauhinia 8: 101–118.

Kaalaas B (1911) Bryophyten aus den Crozet-inseln. I. Nyt Magazin for Naturvidenskaberne 49: 81–98.
Lara F, Draper I, Gariletti R (2023) New insights into the genus *Stoneobryum* (Bryophyta: Orthotrichaceae) based on recent collections of the two known species. Bryophyte Diversity & Evolution 46: 92–108. https://doi.org/10.11646/bde.46.1.13
Lehmann JGC (1829) Hepaticarum capensium a C. F. Ecklon collectarum brevem recensionem. Linnaea 4: 357–371.
Lehmann JGC (1834) Novarum et minus cognitarum stirpium pugillus sextus. Meissner, Hamburg, 1–72.
Lehmann JGC (1844) Novarum et minus cognitarum stirpium pugillus octavus. Meissner, Hamburg, 1–56.
Liu Y, Yan HF, Cao T, Ge XJ (2010) Evaluation of 10 plant barcodes in Bryophyta (Mosses). Journal of Systematics and Evolution 48: 36–46. https://doi.org/10.1111/j.1759-6831.2009.00063.x
Mitten W (1854) Hepaticae. In: Hooker JD (Ed.) The botany of the Antarctic Voyage. II. Flora Novae Zealandiae. Part II. Flowerless plants. Lovell Reeve, London, 125–172.
Mitten W (1867) Hepaticae. In: Hooker JD (Ed.) Handbook of the New Zealand flora, part II. Lovell Reeve, London, 497–549.
Mitten W (1876) The Musci and Hepaticae collected by H. N. Moseley, M. A., Naturalist to H. M. S. "Challenger". Journal of the Linnean Society, Botany 15: 59–73. https://doi.org/10.1111/j.1095-8339.1876.tb00223.x
Mitten W (1877) List of Hepaticae collected by the Rev. A. E. Eaton at the Cape of Good Hope. Journal of the Linnean Society, Botany 16: 187–197. https://doi.org/10.1111/j.1095-8339.1877.tb02316a.x
Mitten W (1884) Juan Fernández and Masafuera. Musci et Hepaticae. In: Hemsley W (Ed.) Report on the scientific results of the voyage of H. M. S. Challenger. Botany Vol. 1, III, part 1. Her Majesty's Stationary Office, London, 78–89.
Montagne CM (1845) Cinquième centurie de plantes cellulaires exotiques nouvelles. Décades VII à X. Annales des Sciences Naturelles, Botanique, sér. 3, 4: 346–367.
Müller K, Müller J, Quandt D (2006) PhyDE - Phylogenetic Data Editor. Program distributed by the authors. http://www.phyde.de/ [accessed 08.08.2024]
Oliveira da Silva FR, Ilkiu-Borges AL, Gradstein SR (2022) Two new Neotropical taxa of *Radula* (Marchantiophyta: Radulaceae) with bordered leaves. Phytotaxa 564: 95–103. https://doi.org/10.11646/phytotaxa.564.1.7
Patiño J, Vanderpoorten A (2018) Bryophyte biogeography. Critical Reviews in Plant Sciences 37: 175–209. https://doi.org/10.1080/07352689.2018.1482444
Perold S (1999) Studies in the Sphaerocarpales (Hepaticae) from southern Africa. 1. The genus *Monocarpus* and its only member, *M. sphaerocarpus*. Bothalia 29: 225–230. https://doi.org/10.4102/abc.v29i2.592
Schäfer-Verwimp A, Pócs T (2009) Contributions to the hepatic flora of the Dominican Republic, West Indies. Acta Botanica Hungarica 51: 367–425.
Schiffner V (1898) Expositio plantarum in itinere suo Indico annis 1893/94 suscepto collectarum. Denkschriften der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse 67: 153–203.
Schiffner V (1900) Die Hepaticae der Flora von Buitenzorg. I. Band. E. J. Brill, Leiden, 1–220.
Schuster RM (2021) Austral Hepaticae III. Nova Hedwigia Beiheft 120: 1–721.
Scott GAM (1985) Southern Australian Liverworts. Australian Flora and Fauna Series 2. Australian Government Publishing Service, Canberra, 1–216.
Scott GAM, Beckmann KG (1987) The biology of *Lethocolea squamata*. Symposia Biologica Hungarica 35: 209–213.
Shaw AJ (2001) Biogeographic patterns and cryptic speciation in bryophytes. Journal of Biogeography 28: 253–261. https://doi.org/10.1046/j.1365-2699.2001.00530.x
Ślipiko M, Myszczyński K, Buczkowska K, Bączkiewicz A, Szczecińska M, Sawicki J (2020) Molecular delimitation of European leafy liverworts of the genus *Calypogeia* based on plastid super-barcodes. BMC Plant Biology 20: 243. https://doi.org/10.1186/s12870-020-02435-y
Spruce R (1882) On *Cephalozia*. Slater, Malton, 1–99.
Spruce R (1885) Hepaticae amazonicae et andinae. II. Transactions and Proceedings of the Botanical Society of Edinburgh 15: 309–588.
Stephani F (1901) Species hepaticarum 2. Bulletin de l'Herbier Boissier, sér. 2 1(10): 1022–1151.
Stephani F (1906) Species hepaticarum 3. Bulletin de l'Herbier Boissier, sér. 2 6(5): 377–392.
Stephani F (1911) Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. II. Die Lebermoose. Kungliga Svenska Vetenskapsakademiens Handlingar, n. ser. 46(9): 1–92.
Stephani F (1916) Hepaticae. In: Herzog T (Ed.) Die Bryophyten meiner zweiten Reise durch Bolivia. Bibliotheca Botanica 87: 1–347.
Stephani F (1917) Species Hepaticarum 6: 1–128. George & Cie, Genève & Bale.
Stephani F (1922) Species Hepaticarum 6: 241–368. George & Cie, Genève & Bale.
Taylor T (1846) New Hepaticae. London Journal of Botany 5: 258–284, 365–417.
Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code). Appendix III: Conserved, Protected and Rejected Names of Genera and Subdivisions of Genera. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten.
Udar R, Kumar A (1986) The genus *Lethocolea* Mitt. from India. Lindbergia 12: 103–105.
Váňa J, Engel JJ (2013) The liverworts and hornworts of the Tristan da Cunha group of islands in the south Atlantic Ocean. Memoirs of the New York Botanical Garden 105: 1–138.
Winkler S (1969) Systematisch-anatomische Untersuchungen über die marsupialen Lebermoose der Sierra Nevada de Santa Marta in Kolumbien. Mitteilungen aus dem Instituto Colombo-Aleman de Investigaciones Cientificas "Punta de Betín" 3: 5–76.
Wynns JT, Lange CBA (2014) A comparison of 16 DNA regions for use as phylogenetic markers in the pleurocarpous moss genus *Plagiothecium* (Hypnales). American Journal of Botany 101: 652–669. https://doi.org/10.3732/ajb.1300269
Zijlstra G (1990) Report of the Committee for Bryophyta: 1. Taxon 39: 289–292. https://doi.org/10.2307/1223053